



저작자표시-비영리-변경금지 2.0 대한민국

이용자는 아래의 조건을 따르는 경우에 한하여 자유롭게

- 이 저작물을 복제, 배포, 전송, 전시, 공연 및 방송할 수 있습니다.

다음과 같은 조건을 따라야 합니다:



저작자표시. 귀하는 원저작자를 표시하여야 합니다.



비영리. 귀하는 이 저작물을 영리 목적으로 이용할 수 없습니다.



변경금지. 귀하는 이 저작물을 개작, 변형 또는 가공할 수 없습니다.

- 귀하는, 이 저작물의 재이용이나 배포의 경우, 이 저작물에 적용된 이용허락조건을 명확하게 나타내어야 합니다.
- 저작권자로부터 별도의 허가를 받으면 이러한 조건들은 적용되지 않습니다.

저작권법에 따른 이용자의 권리는 위의 내용에 의하여 영향을 받지 않습니다.

이것은 [이용허락규약\(Legal Code\)](#)을 이해하기 쉽게 요약한 것입니다.

[Disclaimer](#)

이학박사학위논문

**Distribution of submerged
macrophytes and environmental
conditions in the rivers of
South Korea**

한국의 하천에서 침수식물
분포와 환경 조건

2017 년 8 월

서울대학교 대학원
생명과학부
손덕주

**Distribution of submerged
macrophytes and environmental
conditions in the rivers of
South Korea**

**By
Deokjoo Son**

Advisor: Professor Eun Ju Lee, Ph.D.

August 2017

**School of Biological Sciences
Graduate School
Seoul National University**

Abstract

The river ecosystems in Korea has been greatly altered from lotic to lentic conditions due to large-scale weir construction. The distribution and abundance of submerged macrophytes have been rapidly expanding along five major rivers. Despite the general importance of submerged macrophytes, fast growing and dense submerged macrophytes can have detrimental effects on river ecosystems. Understanding both the species composition of submerged macrophytes and the major environmental factors related to aquatic plants is important for river management. This study focused on identification of the relationships between the submerged macrophytes species and environmental factors. I performed vegetation survey and measured environmental factors at 197 surveyed sites along the five major rivers from May to September, 2014–2015: Han River (71 sites), Geum River (43 sites), Nakdong River (46 sites), Yeongsan River (27 sites), and Seomjin River (10 sites). *Ceratophyllum demersum*, *Hydrilla verticillata*, *Myriophyllum spicatum*, *Najas graminea*, *N. marina*, *Potamogeton crispus*, *P. maackianus*, *P. malaianus*, *P. octandrus*, *P. oxyphyllus*, *P. pusillus*, and *Vallisneria natans*, were distributed in the river regions. The most abundant species of submerged macrophytes in all rivers were *H. verticillata*, *M. spicatum*, and *P. crispus*. Based on the analysis of dissimilarities, species composition of submerged macrophytes and the environmental conditions in the four major rivers (Han, Geum, Nakdong, Yeongsan Rivers) were similar, whereas the occurrence rates (prevalence) of submerged macrophytes differed. However, ammonium nitrogen, nitrate nitrogen, and total nitrogen concentrations were significantly different between the four rivers. In

particular, Han River had higher ammonium nitrogen concentrations and Yeongsan River had lower nitrate nitrogen and total nitrogen concentrations, than the other rivers. Environmental factors associated with the occurrence of submerged macrophytes were related to light availability, such as chlorophyll *a*, suspended solids, and water temperature during the growing season, whereas nutrient concentration was not an important factor. *Najas marina* became established rapidly and was an important species over the three year at two monitoring sites, Yangpyeong site in Han and Sangju site in Nakdong Rivers. According to the comparison of submerged macrophyte diversity among *Ceratophyllum demersum* community, *Hydrilla verticillata* community, *Myriophyllum spicatum* community, *Potamogeton crispus* community, *Vallisneria natans* community, and others community, species in *V. natans* community had relatively even coverage and this community exhibited the highest diversity. From generalized linear models, the ammonium nitrogen and nitrate nitrogen concentrations, and water velocity had the most influence on the Shannon diversity index and species richness, which decreased with high nutrient concentrations and rapid water flow. The results indicated that submerged macrophyte diversity was highest under low productivity and low disturbance conditions. I examined the environmental factors that characterize the potential habitats of two most abundant submerged plants, *Myriophyllum spicatum* and *Hydrilla verticillata*, using generalized additive models. Potential habitats of *M. spicatum* were linked with chlorophyll *a*, nitrate nitrogen, suspended solids, water temperature, water depth, and water velocity. In the case of *H. verticillata*, electrical conductivity and suspended solids were important in determining habitat factors. Monitoring of vegetation and environmental conditions in river ecosystems is important because dispersal and composition of submerged macrophytes are affected

by both water quality factors and water velocity. Preservation of free-flowing rivers with a variety of hydrological features is needed to provide the water quality needed to ensure submerged macrophyte diversity and to control submerged macrophytes abundance to an appropriate level. These results provide information on the initial distribution of submerged macrophytes and on potential submerged macrophytes habitats for the management of river ecosystems after the large-scale weir construction.

Keyword: river ecosystem, submerged macrophytes, water environmental variables,
Hydrilla verticillata, *Myriophyllum spicatum*

Student Number: 2012-30085

Contents

Abstract	i
Contents.....	iv
List of Tables	viii
List of Figures	x
Chapter 1. General introduction.....	1
1.1. Characteristics of submerged macrophytes	2
1.2. Previous research on submerged macrophytes	5
1.3. River flow regulation	7
1.4. Objectives of the study	9
Chapter 2. Distribution of submerged macrophytes and environmental conditions	11
2.1. Introduction.....	12
2.2. Materials and methods.....	14

2.2.1. Study area	14
2.2.2. Data collection	16
2.2.3. Statistical analysis	17
2.3. Results	18
2.3.1. Spatial distribution of submerged macrophytes	18
2.3.2. Comparison of submerged macrophytes species and environmental factors between the four rivers	21
2.3.3. Environmental factors related to occurrence of submerged macrophytes	31
2.4. Discussion	33
2.4.1. Comparison of submerged macrophytes and environmental factors between the four rivers	33
2.4.2. Parameters related to occurrence of submerged macrophytes	34

Chapter 3. The relationships between submerged macrophyte diversity and environmental factors.....38

3.1. Introduction.....	39
3.2. Methods	41
3.2.1. Study area	41
3.2.2. Data collection	43
3.2.3. Diversity index and water quality changes.....	45
3.2.4. Environmental factors influencing the submerged macrophyte community	45
3.2.5. Environmental factors related to submerged macrophyte diversity	46
3.3. Results	49

3.3.1. Changes in importance values of submerged macrophytes and water column conditions.....	49
3.3.2. Multiple factors affecting submerged macrophyte community.....	55
3.3.3. Submerged macrophyte diversity and response to environmental factors	57
3.4. Discussion	63
3.4.1. Establishment and expansion of <i>Najas marina</i>	63
3.4.2. Submerged macrophyte diversity and response to environmental gradients	64

Chapter 4. Potential habitat environment of two submerged macrophytes, *Myriophyllum spicatum* and *Hydrilla* *verticillata*66

4.1. Introduction.....	67
4.2. Materials and methods.....	70
4.2.1. Study sites and data collection.....	70
4.2.2. Model building	70
4.2.3. Validation of the predictive performance of models.....	73
4.3. Results.....	74
4.3.1. GAM response curves.....	74
4.3.2. Model validation and field verification.....	81
4.4. Discussion	84
4.4.1. GAM results and environmental factors	84
4.4.2. Potential habitat predictions.....	87
4.4.3. Perspectives	90

Chapter 5. General conclusion	91
References	97
Appendix	126
국문 초록	150

List of Tables

Table 2-1. List of 12 species of submerged macrophytes included in the study	19
Table 2-2. The frequency of submerged macrophytes in the Geum (43 sites), Han (71 sites), Nakdong (46 sites), Yeongsan (27 sites), and Seomjin (10 sites) Rivers	20
Table 2-3. The importance values of 12 species of submerged macrophytes in the Geum River ($n = 22$).....	24
Table 2-4. The importance values of 12 species of submerged macrophytes in the Han River ($n = 55$).....	25
Table 2-5. The importance values of 12 species of submerged macrophytes in the Nakdong River ($n = 33$).....	26
Table 2-6. The importance values of 12 species of submerged macrophytes in the Yeongsan River ($n = 11$)	27
Table 2-7. Chemical and physical parameters of the water column at sites with and without vegetation	32
Table 3-1. Descriptive statistics for chemical and physical variables of 128 vegetated sites	44
Table 3-2. Pearson correlation coefficients for nine water chemical variables.	48
Table 3-3. Environmental variables related to the Shannon diversity index and species richness by generalized linear models (GLMs)	58
Table 4-1. Mean, standard error (SE), minimum (Min), and maximum (Max) values for physical and chemical properties of water at 197 sites.....	72
Table 4-2. Selected environmental variables and deviance explained in	

generalized additive models (GAMs) for <i>Myriophyllum spicatum</i> and <i>Hydrilla verticillata</i>	76
Table 4-3. Comparison of predicted and observed distributions of <i>Myriophyllum spicatum</i> and <i>Hydrilla verticillata</i> during model building	82
Table 4-4. Comparison of predicted and observed distributions of <i>Myriophyllum spicatum</i> and <i>Hydrilla verticillata</i> at the model confirmation stage.....	83
Appendix 1. Similarity percentage (SIMPER) analyses of submerged macrophytes representing the occurrence (occurrence rate) of major taxa between the four rivers	126
Appendix 2. Similarity percentage (SIMPER) analyses of environmental factors representing the mean and standard error between the four rivers.....	128
Appendix 3. Locations of the 197 surveyed sites and submerged macrophytes coverage.....	130
Appendix 4. Water environmental factors at the 197 surveyed sites	140

List of Figures

Fig. 2-1. Locations of the 197 study sites, including the 71 sites along the Han River, 43 sites along the Geum River, 46 sites along the Nakdong River, 27 sites along the Yeongsan River, and 10 sites along the Seomjin River	15
Fig. 2-2. Detrended correspondence analysis (DCA) ordination of surveyed sites and submerged macrophytes species	23
Fig. 2-3. Boxplots for (A) ammonium nitrogen (NH₄N), (B) nitrate nitrogen (NO₃N), and (C) total nitrogen (TN)	30
Fig. 3-1. Locations of classified submerged macrophyte communities at 128 vegetated sites of submerged macrophytes at the Korean streams.....	42
Fig. 3-2. Changes in importance values of submerged macrophytes for three years at the (A) Yangpyeong site in the Han River and (B) Sangju site in the Nakdong River.....	50
Fig. 3-3. Changes in water quality for eight variables (mean \pm standard error) between 2012 and 2016 at the Yangpyeong site in the Han River	52
Fig. 3-4. Changes in water quality for eight variables (mean \pm standard error) between 2012 and 2016 at the Sangju site in the Nakdong River.....	54
Fig. 3-5. Biplot of canonical correspondence analysis (CCA) ordination of 128 sites that were classified into submerged macrophyte communities.....	56
Fig. 3-6. Comparison of (A) Shannon diversity index and (B) species richness of submerged macrophyte communities	60
Fig. 3-7. Relationships between Shannon diversity index and environmental factors	61
Fig. 3-8. Relationships between species richness and environmental factors ..	62

Fig. 4-1. Response curves of <i>Myriophyllum spicatum</i> for environmental gradients in generalized additive models (GAMs)	77
Fig. 4-2. Response curves of <i>Hydrilla verticillata</i> for environmental gradients in generalized additive models (GAMs).....	78
Fig. 4-3. Predicted and observed habitat suitability of <i>Myriophyllum spicatum</i> based on generalized additive models (GAMs).....	79
Fig. 4-4. Predicted and observed habitat suitability of <i>Hydrilla verticillata</i> based on generalized additive models (GAMs).....	80

Chapter 1. General introduction

1.1. Characteristics of submerged macrophytes

The term submerged macrophytes usually refers to rooted aquatic angiosperms or underwater nonflowering or flowering macrophytes (Moore 2009). Submerged macrophytes occur in freshwater, coastal lagoons, and estuaries (Lirman et al. 2007) and tend to have a broader distribution than terrestrial plants (Santamaría 2002). Discontinuous distribution of submerged macrophytes results from differences in colonization success and spatial variations in frequency and intensity of disturbances (Bunn and Arthington 2002).

Many submerged macrophytes exhibit clonal propagation or perennation under conditions that can limit sexual reproduction, seed production, germination, and seedling establishment (Barrett et al. 1993, Santamaría 2002). Because of the reduced lignification in submerged macrophytes tissues, their vegetative organs are fragile and brittle, thus they are easily broken or fragmented by water flow and animals (Barrat-Segretain 1996). Vegetative organ types of submerged macrophytes include nodes, shoots, rhizomes, stolons, tubers, and turions (Grace 1993, Barrat-Segretain 1996). Vegetative reproduction is common in submerged macrophytes, due to the relative uniformity of aquatic habitats, and is more successful than sexual reproduction (Grace 1993, Barrat-Segretain 1996). The trade-off between vegetative and sexual reproduction methods may be related to differences in the nutrient-storage pool of plants (Yeo 1965, Grace 1993); in general, vegetative reproduction may affect maintenance of a species in one site, whereas sexual reproduction may affect colonization of new sites (Barrat-Segretain 1996).

Submerged macrophytes are able to grow and survive at a maximum water depth of 5–6 m (Welsh and Denny 1980); however, submerged macrophytes rarely

inhabit depths exceeding 2.5 m (Angradi et al. 2013). Water depth influences other environmental factors including light intensity, water temperature variation, and nutrient concentration (Zhou et al. 2016). In addition to light intensity being reduced with increasing depth, water turbidity and dense submerged macrophyte communities may result in less than 4% of surface light reaching plants at depth (Sculthorpe 1985, Barko et al. 1986). Thus, submerged macrophytes occur under a great diversity of light conditions that are affected by optical properties within the water column (Santamaría 2002). Light attenuation in the water column is also affected by phytoplankton abundance (Santamaría 2002).

Aquatic ecosystems are generally considered to have temperature conditions that are more stable than those of terrestrial ecosystems (Bornette and Puijalon 2011). Most submerged macrophytes have a relatively high optimal temperature (between 20 to 35°C) for photosynthesis and respiration (Santamaría and van Vierssen 1997). However, some submerged macrophytes are able to grow and reproduce vegetatively at lower temperatures (Boylen and Sheldon 1976), and the ability of some submerged macrophytes to adapt to lower temperatures may provide them with a competitive advantage (Barko et al. 1986). Water depth in large lakes and ponds can affect seasonal stratification of water temperature, whereas in small or shallow water bodies water temperature can be influenced by waterbody surface area (Bornette and Puijalon 2011).

Submerged macrophytes are associated with substrata and are more heterogeneously distributed where substratum heterogeneity is high (Baatrup-Pedersen and Riis 1999). To anchor submerged macrophytes within an area, some submerged macrophytes need a fine substrate while others need mineral substrate (Bornette and Puijalon 2011). In gravel, some species become anchored so efficiently

that they can withstand relatively high water flow velocities (Puijalon et al. 2005).

Submerged macrophytes are an integral part of the ecosystem as they provide habitat for other organisms, sequester carbon, prevent sediment resuspension, stabilize shoreline areas, and act as food sources for consumers at various trophic levels (Bornette and Puijalon 2011, Zhang et al. 2016). Submerged macrophytes produce oxygen in stagnant regions and prolong the hydrologic retention time for the removal of particulate nutrients (Nepf et al. 2007). Furthermore, submerged macrophytes reduce algal growth by competing for nutrients and releasing allelopathic compounds (Takamura et al. 2003). In addition, submerged macrophytes has important functions in biogeochemical cycles through such actions as organic carbon production, transfer of oxygen and trace elements, and phosphorus assimilation by mycorrhizal associations (Koch 2001, Caraco et al. 2006, Bornette and Puijalon 2011).

Despite the general importance of submerged macrophytes, fast growing and competitive submerged macrophytes can have detrimental effects on water conditions. Dense submerged macrophytes can produce organic materials from actively growing or senescing macrophytes and cause eutrophication (Chambers et al. 1999). Moreover, dense submerged macrophytes can reduce flow velocity resulting in increased particle sedimentation (Sand-Jensen and Vindbæk Madsen 1992). Dense submerged macrophyte communities under high nutrient concentrations can decrease light penetration and dissolved oxygen levels near the waterbody bottom (Takamura et al. 2003) due to the respiratory demands for oxygen of dead plant materials undergoing aerobic bacterial decay (Kelly et al. 1983, Chambers et al. 1999). Additionally, dense submerged macrophytes can impair aesthetics, cause taste and odor problems in drinking water supplies, clog intakes of

pumps used for conveying irrigation, industrial, or domestic water and interfere with swimming and boating activities (Kenneth 1996, Chambers et al. 1999). Based on these problems, dense submerged macrophytes are generally deemed problematic as many of solutions to those problems are challenging.

1.2. Previous research on submerged macrophytes

Fundamental studies on submerged macrophytes in Korea have been undertaken rarely. Initial research on hydrophyte classification in Korea was conducted by Choi (1985), followed by a study of Potamogetonaceae reported by Kim et al. (2002), and a report on Hydrocharitaceae by Na (2010). Floral surveys and studies into the distribution of submerged, riparian and littoral plants have been carried out in local streams (Lee 2009, Cho and Lim 2011), reservoirs (Lim et al. 2005, Kim et al. 2011, Kim et al. 2012), coastal lagoons (Kim et al. 2010) and wetlands (You et al. 2008, Lim et al. 2016). A long-term study reported by Lim (2010) described the distributional patterns of hydrophytes based on previous reports and on field surveys undertaken between 1997 and 2007 on a national scale. Another long-term study reported by Park (2016) described changes in hydrophytes and environmental conditions in the Paldang Reservoir, Gyeonggi Province, Korea occurring between 1988 and 2014. The other studies included soil seed bank experiments on lakebed (Rim 2010) and wetland soils (Yi et al. 2009). To identify the relationships between submerged macrophytes and environmental factors, studies into the effects of floating and submerged plants on water environmental conditions (Lee and Sung 2013) and the growth responses of submerged

macrophytes to environmental conditions (Kwon 2011), have included mesocosm experiments. The underlying relationships between submerged macrophytes and environmental factors have rarely been investigated in the field and there are no previous large- or national-scale studies into submerged macrophytes and environmental factors.

Historically, various classification systems specifically for aquatic plant taxa have been developed (Pearsall 1918, Arber 1920, Den Hartog and Segal 1964). During the past few decades, researchers have identified many characteristics of submerged macrophytes including morphological traits (Lehmann et al. 1997), along with life (Kautsky 1988), reproductive, and dispersal (Barrat-Segretain 1996) strategies. The dispersal ability of submerged macrophytes varies according to the dispersal-related functional traits of each species, such as their reproductive mode and growth characteristics (Capers et al. 2010). Some studies have focused on interactions among submerged macrophytes growth, sediment nutrient status (Barko et al. 1991, Xie et al. 2013), and interspecific competition for resource use (McCreary 1991).

Several studies have focused on the general relationships between submerged macrophytes and local environmental characteristics, particularly those related to water chemistry (Seddon 1972, Sand-Jensen 1977, Carpenter 1980, Depew et al. 2011). Researchers have reported that not only water chemistry, but also various environmental factors including spatial heterogeneity (Pollock et al. 1998), landscape features (Cheruvilil and Soranno 2008), shoreline armoring (Patrick et al. 2016), wave movement (Madsen et al. 2001) and disturbance such as flood frequencies and weed cutting (Riis et al. 2000) can affect distribution and diversity of submerged macrophytes.

Moreover, submerged macrophytes have been used as a bioindicator of water quality (Clayton and Edwards 2006), ecological health (Maddock 1999) and river connectivity (Rooney et al. 2013). Habitat requirements of submerged macrophytes have been included as factors in diagnostic tools used to assess the suitability of an area for submerged macrophytes restoration (Michael Kemp et al. 2004). Additionally, ecological engineering studies have reported on the effects of submerged macrophytes on heavy metal adsorption (St-Cyr et al. 1994, Keskinen et al. 2004) and nutrient removal (Dierberg et al. 2005). Recent studies have estimated the distribution of submerged macrophytes in many areas by using geographic information system (GIS)-based approaches and a combination of remote sensing and complex models under different scenarios of environmental condition change (Alahuhta et al. 2011, Abukawa et al. 2013, Zhang et al. 2015, Churchill et al. 2016); however, these studies have been limited to examining lakes (Abukawa et al. 2013, Zou et al. 2013), bays (Depew et al. 2011, Patrick et al. 2014) and estuaries (Borgnis and Boyer 2016, Hestir et al. 2016). In the mainstreams of rivers, research into distribution of submerged macrophytes has rarely conducted. River ecosystems are substantially dynamic; thus their substrata may be too changeable to use GIS mapping to predict distribution of submerged macrophytes.

1.3. River flow regulation

Rivers are important pathways for the flow of organisms, materials, and energy (Andersson et al. 2000) and many in-river and riparian corridor plants are dispersed by water flow (Johansson et al. 1996). The natural flow regime of a river sustains

ecosystem biodiversity and integrity via temporal and spatial variability, thereby forming heterogeneous habitats and producing natural changes in species composition (Baatrup-Pedersen and Riis 1999, Nilsson and Svedmark 2002).

Currently, flow regulation through widespread stream channelization and damming is a common characteristic of many Korean rivers (Woo 2010), thus it is difficult to find lotic systems (Choi et al. 2011). Extensive river flow changes in Korea since the 1960s have accelerated the degradation (Woo 2010) and eutrophication (Kim et al. 2007) of rivers. Recently in Korea, changes to the flow regime and water quality of four major river systems were undertaken as part of “The Four Major Rivers Project”. The goals of this national project were to reduce flooding, improve water quality, and secure water resources by constructing three dams and 16 large weirs (Lah et al. 2015).

Many rivers throughout the world have been fragmented and their flows regulated by the construction of dams and weirs over the past century (Andersson et al. 2000, Schook et al. 2016). The construction of dams and weirs in rivers is regarded as a key threat to aquatic biodiversity (Mueller et al. 2011) as dam- or weir-induced flow regulation alters river discharge, sediment flux, and floodplain productivity, and it decouples ecological interactions between the river and its floodplain (Dynesius and Nilsson 1994, Nilsson et al. 2005, Schook et al. 2016). Additionally, a modified flow regime results in serial discontinuity in plant, fish, zooplankton, and macroinvertebrate distributions (Zhou et al. 2008). Moreover, it results in increased macrophyte abundance, excessive submerged macrophytes growth (Bunn and Arthington 2002), and impoverished habitats for organisms adapted to a natural discharge regime (Dynesius and Nilsson 1994). In regulated rivers, the abundance and recruitment of native fishes is altered (Humphries et al.

2008), and fish species diversity is decreased (Gehrke et al. 1995). Macroinvertebrate populations also exhibit declines in taxon richness and interspecies abundance shifts due to river flow regulation (Holt et al. 2015). In particular, when weirs interrupt a river's longitudinal pathway, plant communities become fragmented and plant dispersal is reduced (Nilsson and Svedmark 2002).

1.4. Objectives of the study

The 12 species of submerged macrophytes included in this study (*Ceratophyllum demersum*, 붕어마름; *Hydrilla verticillata*, 검정말; *Myriophyllum spicatum*, 이삭물수세미; *Najas graminea*, 나자스말; *N. marina*, 민나자스말; *Potamogeton crispus*, 말즘; *P. maackianus*, 새우가래; *P. malaianus*, 대가래; *P. octandrus*, 애기가래; *P. oxyphyllus*, 말; *P. pusillus*, 실말 and *Vallisneria natans*, 나사말) are distributed in river regions that are within their environmental condition tolerances. These species are cosmopolitan angiosperms with extensive worldwide ranges (Zhou et al. 2016). Because of the widespread and extensive submerged macrophytes increases since large-scale weir construction was undertaken, this study focused on identification of the relationships between the submerged macrophytes and environmental factors in four major Korean rivers.

In chapter 2, the distribution of submerged macrophytes and environmental conditions in the five rivers are described. In addition, the prime environmental factors related to occurrence of submerged macrophytes in those rivers are demonstrated.

In chapter 3, short-term changes in submerged macrophyte communities and

water column conditions at monitoring sites are described. Additionally, environmental gradient factors that significantly influenced submerged macrophytes community structure and diversity are identified.

In chapter 4, due to the explicit links between submerged macrophytes and water quality, predicting the distribution of potential habitats for submerged macrophytes in the four rivers is undertaken by using occurrence data for the two most abundant submerged macrophytes, *Myriophyllum spicatum* and *Hydrilla verticillata*.

Chapter 2. Distribution of submerged macrophytes and environmental conditions

2.1. Introduction

Natural rivers in temperate climates display seasonal fluctuations in water levels and discharge levels (Hudon 1997). Physical barriers such as weirs and dams disrupt these natural variations and alter the aquatic community structure and habitat quality (Almeida et al. 2009, Mueller et al. 2011). Throughout the world, river ecosystems have been fragmented, degraded, and threatened (Manolaki and Papastergiadou 2016). Recently, in Korea, the flow regime and water quality of major river ecosystems has been changed by “The Four Major Rivers Project” (2009–2012). The goals of this national project were to reduce flooding, improve water quality, and secure water resources by constructing three dams and 16 large weirs (Lah et al. 2015). The natural flow regime has been greatly altered from lotic to lentic conditions, and submerged macrophytes have become widely distributed throughout the river ecosystems in Korea. Flow regime is a major determinant of physical habitats in streams and rivers, which in turn regulates biotic composition (Bunn and Arthington 2002). The effectiveness of the river project is currently subject to debate, so ecological monitoring of submerged macrophytes and environmental conditions in the newly altered flow regime is necessary.

Dams and weirs modify natural flow regimes and reduce regional differences and environmental heterogeneity across broad geographic scales (Poff et al. 2007). Regional homogenization also changes (increases or decreases) local species diversity (Johnson et al. 2014). A reduction in water flow variability reduces channel complexity and leads to homogeneity of aquatic habitats, fish fauna, and native species community (Moyle and Mount 2007). Habitat loss reduces species diversity by increasing ecosystem homogeneity, which reduces the numbers of plant species

within aquatic communities (Airoldi et al. 2008, Johnson et al. 2014). This process is defined as biotic homogenization (McKinney and Lockwood 1999).

Most species of submerged macrophytes are usually dispersed by vegetative parts and seeds that are buoyant and move long distances through flowing water (Riis and Sand-Jensen 2006). These dispersals are driven primarily by unidirectional downstream flow, which causes the offspring plants to migrate far away from the parental plants (Liu et al. 2006, Riis and Sand-Jensen 2006). However, the construction of dams and weirs transforms flowing rivers into stairs of fragmented lake-like water bodies, which severely disrupts the dispersal of waterborne diaspores of vascular plants (Jansson et al. 2000) and vegetative propagules that are detached by strong flow (Riis and Sand-Jensen 2006). Furthermore, water flow regulation affects the natural riverine soil seed bank dynamics (Greet et al. 2013) and reduces native plant cover in riparian wetlands (Catford et al. 2011).

Submerged macrophytes occurrence was observed accidentally, although submerged macrophytes inhabit in the same water corridor and under limited dispersal conditions. The submerged macrophytes occurrence was assumed to have been caused by local environmental factors. Light availability (Michael Kemp et al. 2004), temperature (Rooney and Kalff 2000), nutrients (Chambers and Kalff 1987), and sediment composition (Jones et al. 2012) are recognized as physical and chemical factors limiting submerged macrophyte establishment, survival, and growth. However, no previous studies in Korea have examined submerged macrophyte occurrence and environmental factors in major rivers and streams. Flora surveys of submerged and riparian plants were conducted only in local streams (Lee 2009) and wetland (You et al. 2008). In this study, using an intensive field survey, I report the distribution of submerged macrophytes and environmental conditions in

the five rivers, Han River, Geum River, Nakdong River, Yeongsan River and Seomjin River.

An essential step in the river management is identifying the distribution patterns of submerged macrophytes, and environmental factors related to submerged macrophytes. In this study, I characterized the submerged macrophytes distribution and the environmental factors in the water columns. I also demonstrate dissimilarities in submerged macrophytes distribution and environmental factors between the rivers. To achieve these goals, the following three questions were posed (1) How distinct are submerged macrophytes distributions and environmental factors in the four rivers? (2) Which plants and environmental factors contribute the dissimilarities between the rivers? (3) What are the prime environmental factors related to submerged macrophytes occurrence, irrespective of environmental condition in each river?

2.2. Materials and methods

2.2.1. Study area

This study was conducted during two growing seasons (May–September, 2014–2015) in the following five major rivers of Korea (33–39° N, 124–130° E): Han River (34,428 km², basin area), Geum River (9,914 km²), Nakdong River (23,690 km²), Yeongsan River (3,469 km²), and Seomjin River (4,914 km²) (WAMIS, http://www.wamis.go.kr/eng/WKB_BSNSP_LST.aspx). The climate is temperate, with an annual mean temperature of 10–14°C and mean annual precipitation of 1,200–1,300 mm (Korea Meteorological Administration), and most rain occurs

during the summer (June–August). Vegetation surveys were conducted at 197 chosen sites in the rivers and tributaries, including 71 sites in the Han River, 43 sites in the Geum River, 46 sites in the Nakdong River, 27 sites in the Yeongsan River, and 10 sites in the Seomjin River (Fig. 2-1). These sites were assigned to water quality monitoring towers operated by the Ministry of Environment.

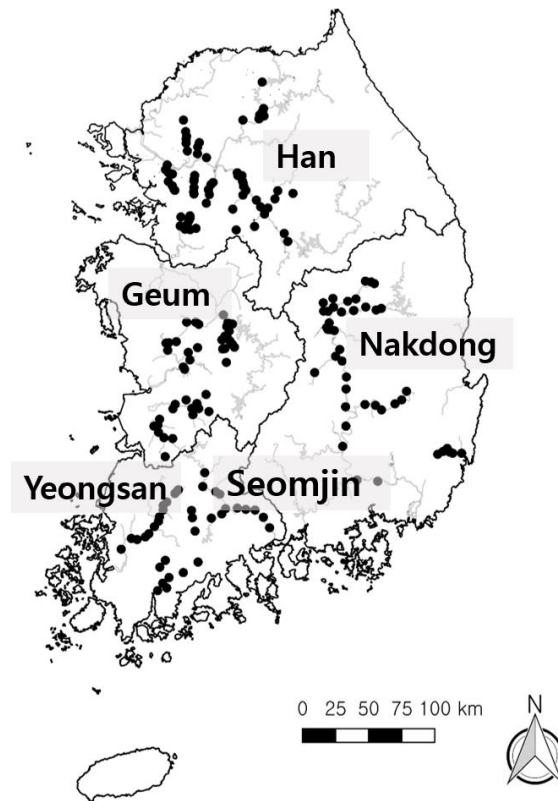


Fig. 2-1. Locations of the 197 study sites, including the 71 sites along the Han River, 43 sites along the Geum River, 46 sites along the Nakdong River, 27 sites along the Yeongsan River, and 10 sites along the Seomjin River.

2.2.2. Data collection

Monthly water quality data were compiled from the Ministry of Environment's national water quality measurement network (<http://water.nier.go.kr>) and averaged from January 2012 to October 2015. Some study sites were not assigned to water quality monitoring towers, and these sites were matched to the nearest monitoring towers within 5 km. Water chemical parameters, including biochemical oxygen demand (BOD), chlorophyll *a*, ammonium nitrogen, nitrate nitrogen, suspended solids, total nitrogen, total dissolved phosphorous, total organic carbon, and total phosphorus are known to be important submerged macrophytes. Chlorophyll *a* and suspended solids in water condition represent the influence of light availability (Koch 2001, Rooney et al. 2013). In particular, chlorophyll *a* is used as a proxy for total phytoplankton biomass (Arthaud et al. 2013). Ammonium nitrogen, nitrate nitrogen, total nitrogen, total dissolved phosphorous, and total phosphorus indicates the role of nutrients, and contribute to the eutrophication of a water body (Hwang et al. 2016). BOD means the amount of dissolved oxygen required by aerobic microbial organisms in water to break down organic matters; higher values of BOD mean higher polluted water conditions (Hwang et al. 2016).

Vegetation surveys were conducted, and presence-absence of each species was recorded using a belt transect (50×2 m) positioned 1 m apart from the edge of river in the direction of river flow (Dawson et al. 1999, Riis et al. 2001), while taking into consideration that submerged macrophytes rarely inhabit depths exceeding 2.5 m (Angradi et al. 2013). The presence/absence of submerged macrophytes species at each site was surveyed by direct observation through the water surface and sampling with a rake for confirmation (Gurnell et al. 2010). All species were identified using, Choi (2000), Kim et al. (2002), Lee (2003), Na (2010) and "The Korean Plant Names

Index (KPNI)” database (www.nature.go.kr/ekpni/SubIndex.do). I also conducted three measurements of water depth and water velocity, which were then averaged. Water velocity (Flowwatch; JDC Electronic SA, Yverdon-les-Bains, Switzerland) and water depth (meter stick) in each transect were measured where vegetation was most abundant. If submerged macrophytes were absent from the selected sites, the belt transect was spaced 1 m apart from the edge of river, and water depth and water velocity were measured in triplicate at the midpoint of transect.

2.2.3. Statistical analysis

Statistical analyses were performed using the R program (R Development CoreTeam 2016). To determine whether composition of submerged macrophytes differed between the four rivers (Han, Geum, Nakdong, and Yeongsan Rivers), the following analytical procedures were conducted. Data from Seomjin River was excluded because of low sample size. Species presence-absence data were fitted along with the four rivers using detrended correspondence analysis (DCA) (Bastow Wilson 2012) and the “envfit” function with 999 permutations (Alday et al. 2011). Standard deviation ellipses were defined for river positions on the biplot. For each four rivers, the importance value was calculated for each species (importance value = relative cover + relative frequency) (Schlising and Sanders 1982). To test the statistical significance of differences between species composition of submerged macrophytes in the rivers, permutational multivariate analysis of variance (PERMANOVA) was performed using distance matrices (“adonis” function in vegan package) (Oksanen et al. 2013) with the Bray-Curtis index (Ross et al. 2012). When PERMANOVA manifested significant differences between the rivers, the similarity percentages (SIMPER, “simper” function in vegan package) (Oksanen et al. 2013)

were analyzed using species presence-absence data to identify the differences in species composition and environmental factors between the rivers (Florentine et al. 2013). The statistical significance of differences between two rivers was calculated using Mann-Whitney *U* test (Coccia et al. 2016). Environmental factors for SIMPER analysis were transformed with $\log(x + 1)$ to reduce the influence of high values between variables. To elucidate the main environmental factors related to occurrence of submerged macrophytes, I performed Student's *t*-test between sites with and without submerged macrophytes.

2.3. Results

2.3.1. Spatial distribution of submerged macrophytes

The 12 different species of submerged macrophytes in 128 of the 197 surveyed sites were identified (Table 2-1). The occurrence of *Myriophyllum spicatum* was highest in the five rivers, followed by *Hydrilla verticillata*, *Potamogeton crispus*, *Ceratophyllum demersum*, *P. malaianus*, and *Vallisneria natans*. By contrast, *Najas graminea*, *P. octandrus*, *P. oxyphyllus*, and *P. pusillus* were rare species that were identified in fewer than ten sites in the five rivers (Table 2-2). The primary species that were abundant in the five rivers were as follows: *M. spicatum* and *H. verticillata* in the Geum River; *M. spicatum* and *P. crispus* in the Han River; *M. spicatum*, *P. crispus*, *H. verticillata*, and *C. demersum* in the Nakdong River; *H. verticillata* and *N. marina* in the Yeongsan River; *H. verticillata* in the Seomjin River. *Hydrilla verticillata* was relatively evenly distributed in the five rivers. All 12 species were distributed in the Han River, whereas ten species were distributed in the Geum and

Yeongsan Rivers, nine species in Nakdong River, four species in Seomjin River.

Table 2-1. List of 12 species of submerged macrophytes included in the study

Scientific name (Korean name)	Life form
Ceratophyllaceae (붕어마름과)	
<i>Ceratophyllum demersum</i> (붕어마름)	Perennial
Haloragaceae (개미탑과)	
<i>Myriophyllum spicatum</i> (이삭물수세미)	Perennial
Hydrocharitaceae (자라풀과)	
<i>Hydrilla verticillata</i> (검정말)	Perennial
<i>Vallisneria natans</i> (나사말)	Perennial
Najadaceae (나자스말과)	
<i>Najas graminea</i> (나자스말)	Annual
<i>Najas marina</i> (민나자스말)	Annual
Potamogetonaceae (가래과)	
<i>Potamogeton crispus</i> (말즘)	Perennial
<i>Potamogeton maackianus</i> (새우가래)	Perennial
<i>Potamogeton malaianus</i> (대가래)	Perennial
<i>Potamogeton octandrus</i> (애기가래)	Perennial
<i>Potamogeton oxyphyllus</i> (말)	Perennial
<i>Potamogeton pusillus</i> (실말)	Perennial

Table 2-2. The frequency of submerged macrophytes in the Geum (43 sites), Han (71 sites), Nakdong (46 sites), Yeongsan (27 sites), and Seomjin (10 sites) Rivers. The relative frequency is shown in parentheses

Species	Geum River	Han River	Nakdong River	Yeongsan River	Seomjin River
<i>Ceratophyllum demersum</i>	4 (0.06)	11 (0.07)	19 (0.18)	3 (0.09)	0 (0)
<i>Hydrilla verticillata</i>	11 (0.18)	22 (0.14)	20 (0.19)	9 (0.28)	7 (0.58)
<i>Myriophyllum spicatum</i>	12 (0.19)	42 (0.27)	24 (0.22)	4 (0.13)	1 (0.08)
<i>Najas graminea</i>	0 (0)	1 (0.01)	0 (0)	0 (0)	0 (0)
<i>Najas marina</i>	4 (0.06)	2 (0.01)	6 (0.06)	9 (0.28)	0 (0)
<i>Potamogeton crispus</i>	10 (0.16)	28 (0.18)	21 (0.20)	0 (0)	3 (0.25)
<i>Potamogeton maackianus</i>	4 (0.06)	15 (0.09)	2 (0.02)	1 (0.03)	0 (0)
<i>Potamogeton malaianus</i>	6 (0.10)	12 (0.08)	7 (0.07)	3 (0.09)	1 (0.08)
<i>Potamogeton octandrus</i>	0 (0)	5 (0.03)	0 (0)	1 (0.03)	0 (0)
<i>Potamogeton oxyphyllus</i>	1 (0.02)	3 (0.02)	2 (0.02)	1 (0.03)	0 (0)
<i>Potamogeton pusillus</i>	4 (0.06)	4 (0.03)	0 (0)	0 (0)	0 (0)
<i>Vallisneria natans</i>	6 (0.10)	13 (0.08)	6 (0.06)	1 (0.03)	0 (0)
Total	62 (1)	158 (1)	107 (1)	32 (1)	12 (1)

2.3.2. Comparison of submerged macrophytes species and environmental factors between the four rivers

The four rivers overlaid on the DCA biplot (gradient length 1 = 3.45, gradient length 2 = 4.25) are presented using species presence-absence data (Fig. 2-2). The first two axes in the DCA ordination explained a total of 57% variation between the rivers. The river ellipses overlapped with each other; however, the PERMANOVA analysis using “adonis” function indicated that vegetation composition differed significantly between the four rivers ($r^2 = 0.12$, $p = 0.001$).

Results from importance values suggest that some species were more likely to be dominant in the four rivers: *Myriophyllum spicatum* and *Hydrilla verticillata*. *Myriophyllum spicatum*, *H. verticillata*, and *Potamogeton crispus* in the Geum and Han Rivers were important species (Table 2-3 and 2-4). *Ceratophyllum demersum* and *P. crispus* in the Nakdong River were also important species (Table 2-5). In the Yeongsan River, *Najas marina* was the dominant species (Table 2-6).

The species presence-absence data were analyzed using SIMPER, which revealed vegetation dissimilarities between the four rivers (Appendix 1). The species composition between rivers were similar, whereas occurrence rates (prevalence) were primarily responsible for the observed variations in dissimilarity between rivers. The SIMPER analysis indicated that species composition was most dissimilar in the Han and Yeongsan Rivers (similarity = 25%), whereas the greatest similarity in species composition was observed in the Han and Nakdong Rivers (similarity = 42%). *Najas marina*, *Hydrilla verticillata*, *Myriophyllum spicatum*, and *Potamogeton crispus* primarily accounted for the dissimilarities in the Han and Yeongsan Rivers, whereas *Ceratophyllum demersum*, *H. verticillata* and *N. marina*

primarily accounted for the dissimilarities in the Han and Nakdong Rivers.

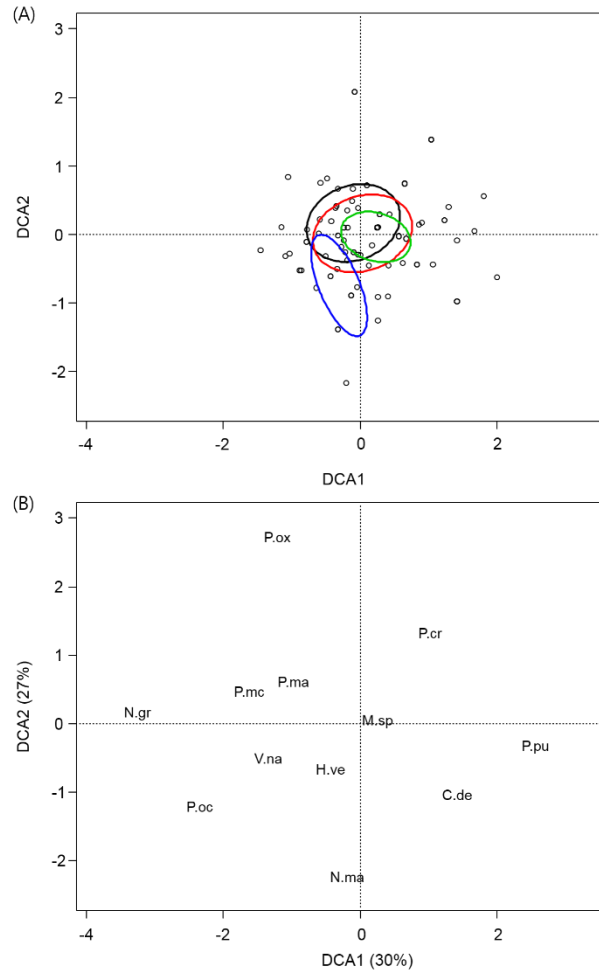


Fig. 2-2. Detrended correspondence analysis (DCA) ordination of surveyed sites and submerged macrophytes species. (A) Open circles represent 121 sites with submerged macrophytes. The four ellipses represent four rivers based on the standard deviations: black, Han River; red, Geum River; green, Nakdong River; blue, Yeongsan River. (B) The observed submerged macrophytes species included C.de, *Ceratophyllum demersum*; H.ve, *Hydrilla verticillata*; M.sp, *Myriophyllum spicatum*; N.gr, *Najas graminea*; N.ma, *N. marina*; P.cr, *Potamogeton crispus*; P.ma, *P. malaiianus*; P.mc, *P. maackianus*; P.oc, *P. octandrus*; P.ox, *P. oxyphyllus*; P.pu, *P. pusillus*; and V.na, *Vallisneria natans*

Table 2-3. The importance values of 12 species of submerged macrophytes in the Geum River ($n = 22$)

Species	Importance value
<i>Myriophyllum spicatum</i>	0.305
<i>Hydrilla verticillata</i>	0.193
<i>Potamogeton crispus</i>	0.165
<i>Vallisneria natans</i>	0.092
<i>Potamogeton malaianus</i>	0.068
<i>Potamogeton pusillus</i>	0.055
<i>Ceratophyllum demersum</i>	0.051
<i>Najas marina</i>	0.044
<i>Potamogeton maackianus</i>	0.021
<i>Potamogeton oxyphyllus</i>	0.005
<i>Najas graminea</i>	0.000
<i>Potamogeton octandrus</i>	0.000

Table 2-4. The importance values of 12 species of submerged macrophytes in the Han River ($n = 55$)

Species	Importance value
<i>Myriophyllum spicatum</i>	0.404
<i>Potamogeton crispus</i>	0.182
<i>Hydrilla verticillata</i>	0.113
<i>Ceratophyllum demersum</i>	0.061
<i>Potamogeton malaianus</i>	0.059
<i>Potamogeton maackianus</i>	0.054
<i>Vallisneria natans</i>	0.053
<i>Potamogeton pusillus</i>	0.030
<i>Potamogeton octandrus</i>	0.019
<i>Potamogeton oxyphyllus</i>	0.017
<i>Najas marina</i>	0.008
<i>Najas graminea</i>	0.002

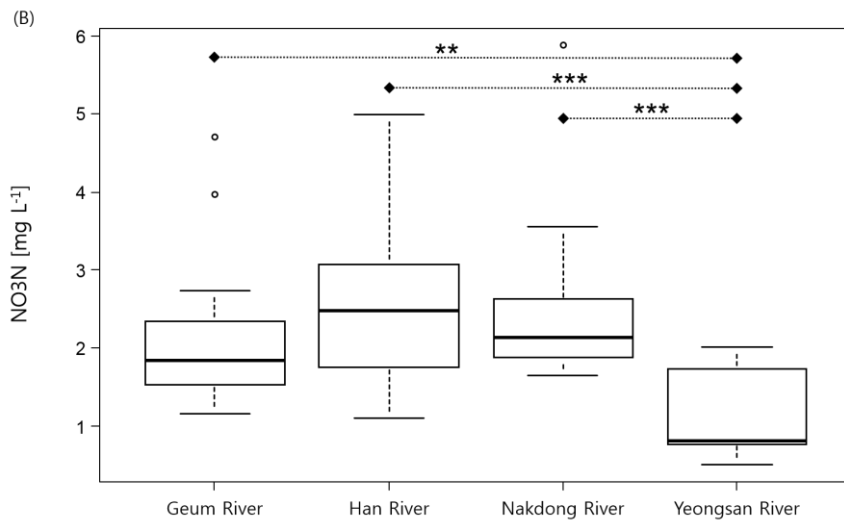
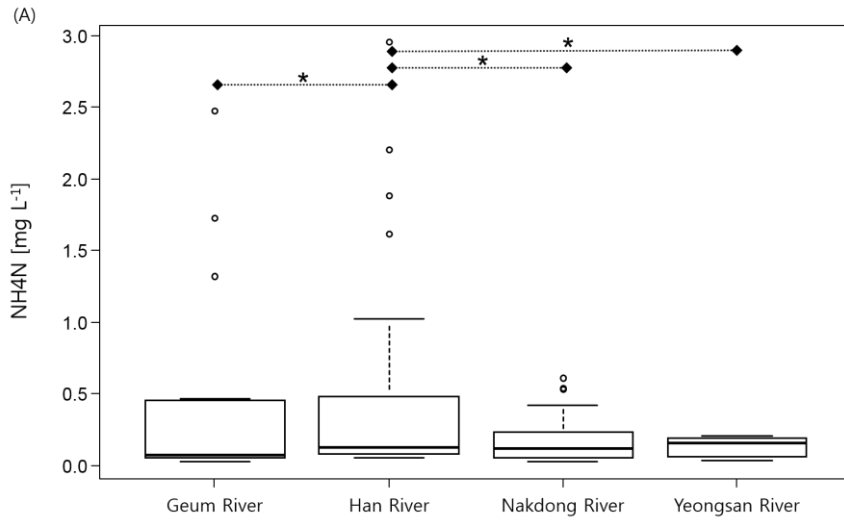
Table 2-5. The importance values of 12 species of submerged macrophytes in the Nakdong River ($n = 33$)

Species	Importance value
<i>Myriophyllum spicatum</i>	0.290
<i>Ceratophyllum demersum</i>	0.216
<i>Hydrilla verticillata</i>	0.176
<i>Potamogeton crispus</i>	0.156
<i>Vallisneria natans</i>	0.063
<i>Potamogeton malaianus</i>	0.038
<i>Najas marina</i>	0.032
<i>Potamogeton maackianus</i>	0.017
<i>Potamogeton oxyphyllus</i>	0.013
<i>Najas graminea</i>	0.000
<i>Potamogeton pusillus</i>	0.000
<i>Potamogeton octandrus</i>	0.000

Table 2-6. The importance values of 12 species of submerged macrophytes in the Yeongsan River ($n = 11$)

Species	Importance value
<i>Hydrilla verticillata</i>	0.333
<i>Najas marina</i>	0.300
<i>Myriophyllum spicatum</i>	0.202
<i>Potamogeton malaianus</i>	0.056
<i>Ceratophyllum demersum</i>	0.054
<i>Potamogeton octandrus</i>	0.021
<i>Potamogeton oxyphyllus</i>	0.012
<i>Potamogeton maackianus</i>	0.012
<i>Vallisneria natans</i>	0.009
<i>Najas graminea</i>	0.000
<i>Potamogeton crispus</i>	0.000
<i>Potamogeton pusillus</i>	0.000

SIMPER analysis of environmental factors (Appendix 2) indicated that environmental factors do not remarkably contribute to dissimilarities between the rivers. The similarities of environmental factors between the rivers ranged from 79% (Geum-Yeongsan Rivers and Han-Yeongsan Rivers) to 81% (Han-Nakdong Rivers). Although decisive dissimilarities between environmental factors were not identified, ammonium nitrate, nitrate nitrogen, and total nitrogen were significantly different between the rivers (Fig. 2-3). The Han River had higher ammonium nitrogen concentrations, and the Yeongsan River had lower nitrate nitrogen and total nitrogen concentrations than the other rivers.



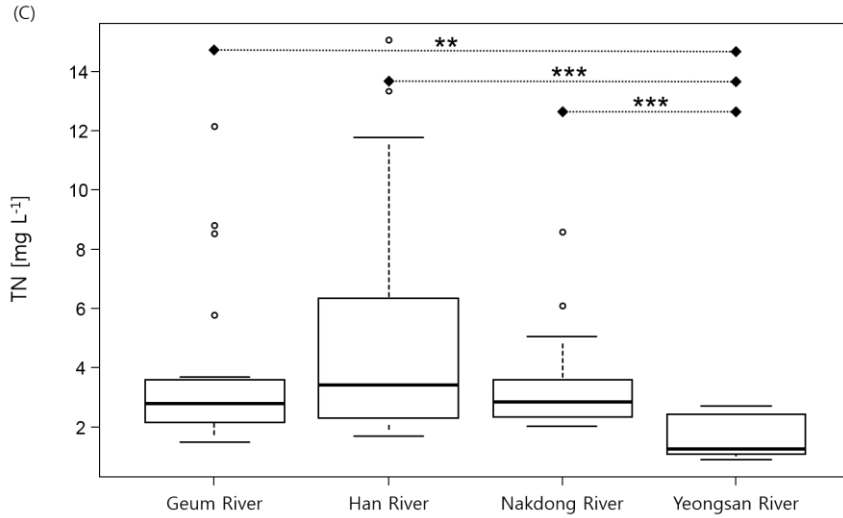


Fig. 2-3. Boxplots for (A) ammonium nitrogen (NH₄N), (B) nitrate nitrogen (NO₃N), and (C) total nitrogen (TN). Boxplots encompass the 25% and 75% quartiles; the central solid lines represent the median. Bars extend to the 95% confidence limits; open circles identify outliers. Significant differences in environmental factor values between rivers were determined by the Mann-Whitney *U* test. Connecting lines show significant differences between rivers; ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$. Geum River ($n = 22$); Han River ($n = 55$); Nakdong River ($n = 33$); and Yeongsan River ($n = 11$).

2.3.3. Environmental factors related to occurrence of submerged macrophytes

The main chemical and physical parameters of the water column are presented in Table 2-7. BOD, chlorophyll *a* (used as a proxy for total phytoplankton biomass), suspended solids, and water temperature during the growing season were significantly higher in sites without submerged macrophytes ($p < 0.004$). In particular, the mean values of chlorophyll *a* and suspended solids were two-fold higher at non-vegetated sites than at vegetated sites.

Table 2-7. Chemical and physical parameters of the water column at sites with and without vegetation. Environmental parameters are presented as means \pm standard errors of monthly measurements from 2012–2015. Water temperature (WT) was calculated during the growing season (May–October), and water depth (WD) and velocity (WV) were measured on the sampling date. Bold text indicates significant differences ($p < 0.001$) by Student's *t*-test between sites with and without vegetation

Parameter	Sites with vegetation ($n = 128$)		Sites without vegetation ($n = 69$)		<i>p</i> -value
	Mean \pm SE	Range	Mean \pm SE	Range	
BOD [mg L⁻¹]	2.2 \pm 0.2	0.6–14.3	3.1 \pm 0.2	0.6–9.8	0.004
Chla [mg m⁻³]	10.7 \pm 0.7	2.1–45.4	20.6 \pm 2.1	0.8–65.0	<0.001
NH ₄ N [mg L ⁻¹]	0.70 \pm 0.14	0.03–8.23	0.80 \pm 0.12	0.02–4.25	0.063
NO ₃ N [mg L ⁻¹]	2.26 \pm 0.09	0.51–5.88	2.26 \pm 0.11	0.54–4.03	0.985
SS [mg L⁻¹]	7.7 \pm 0.4	1.2–31.6	13.1 \pm 0.9	1.1–35.6	<0.001
TDP [mg L ⁻¹]	0.07 \pm 0.01	0.01–1.26	0.09 \pm 0.01	0.01–0.60	0.334
TN [mg L ⁻¹]	3.78 \pm 0.24	0.91–15.05	3.86 \pm 0.24	0.86–10.08	0.152
TOC [mg L ⁻¹]	3.12 \pm 0.14	0.94–11.77	3.81 \pm 0.22	1.16–9.25	0.844
TP [mg L ⁻¹]	0.10 \pm 0.01	0.02–1.51	0.12 \pm 0.01	0.02–0.74	0.214
WT [°C]	22.8 \pm 0.2	17.7–25.5	23.6 \pm 0.1	20.2–26.0	<0.001
WD [m]	0.61 \pm 0.03	0.15–1.60	0.62 \pm 0.04	0.10–1.20	0.960
WV [m s ⁻¹]	0.09 \pm 0.01	0.00–0.90	0.13 \pm 0.02	0.00–0.83	0.960

Note: Biochemical oxygen demand (BOD), chlorophyll *a* (Chla), ammonium nitrogen (NH₄N), nitrate nitrogen (NO₃N), suspended solids (SS), total dissolved phosphorous (TDP), total nitrogen (TN), total organic carbon (TOC), total phosphorus (TP), water depth (WD), water velocity (WV).

2.4. Discussion

2.4.1. Comparison of submerged macrophytes and environmental factors between the four rivers

This research identified differences in distributions of submerged macrophytes and environmental factors between the four major rivers in Korea, and determined the relationships between environmental factors and occurrence of submerged macrophytes. The most abundant species in the four rivers, *Myriophyllum spicatum*, *Hydrilla verticillata*, and *Potamogeton crispus*, have the ability to tolerate wide differences in environmental conditions and to displace other plants (Kenneth 1996, Takamura et al. 2003). The seven major aquatic plant species contributing to vegetation dissimilarities observed in these rivers included *H. verticillata*, *M. spicatum*, *Ceratophyllum demersum*, *P. crispus*, *Najas marina*, *P. maackianus*, and *P. pusillus*. However, environmental factors did not remarkably differ between the rivers. Although environmental factors were highly similar, I detected significant differences between the four rivers with respect to ammonium nitrogen, nitrate nitrogen, and also in total nitrogen concentration. The Yeongsan River had lower nitrate nitrogen and total nitrogen concentrations that were distinct from those of other rivers, although the sample size of the Yeongsan River was limited.

Although there were dissimilar in occurrence rates (prevalence) of submerged macrophytes between the surveyed rivers, species composition and environmental conditions across rivers are homogeneous.

2.4.2. Parameters related to occurrence of submerged macrophytes

Occurrence of submerged macrophytes in the observed sites was related to the levels of BOD, chlorophyll *a*, suspended solids, and the water temperature during the growing season. It was difficult to demonstrate the cause-effect relationship between establishment or occurrence of submerged macrophytes, and environmental conditions. However, BOD, chlorophyll *a*, suspended solids, and water temperature were significantly different in sites with and without submerged macrophytes. These critical parameters, which are directly or indirectly related to light availability for photosynthesis, were higher at sites without submerged macrophytes than at sites with submerged macrophytes. Similar to this findings, Søndergaard et al. (2010) found that chlorophyll *a* and suspended solids concentration had negative relationships with macrophyte coverage and volume.

Chlorophyll *a* is a photosynthetic pigment present in phototrophs such as phytoplankton, algae, and cyanobacteria (Gregor and Maršálek 2004). It is commonly used as a proxy for total phytoplankton biomass, which is strongly related to nutrient content (Arthaud et al. 2013). Phytoplankton grow fast, require substantial amounts of nutrients, and compete with periphyton and macrophytes for light and nutrients (Sand-Jensen and Borum 1991). These results for chlorophyll *a* were consistent with data obtained by Takamura et al. (2003), which showed that chlorophyll *a* concentrations were significantly lower in sites with submerged macrophytes than in sites without submerged macrophytes. Increased nutrient loading has a crucial role in freshwater ecosystems in the shift of water from a macrophyte-dominated clear state to a phytoplankton-dominated turbid state.

Therefore, phytoplankton dynamics should be examined with respect to the presence or absence of submerged macrophytes (Takamura et al. 2003, Sultana et al. 2010). Moreover, growth and distribution of submerged macrophytes rely on periphyton colonization of plant surfaces, which inhibits plant nutrient uptake and photosynthesis (Sand-Jensen 1977, Sultana et al. 2010).

Suspended solids are the mass or concentration of fine organic and inorganic matter, and turbidity is often used as a proxy measure of suspended solids (Bilotta and Brazier 2008). Physical and chemical alterations caused by suspended solids include reduced light penetration, temperature changes, oxygen shortages, and release of contaminants (Ryan 1991, Kronvang et al. 2003, Bilotta and Brazier 2008). Light has been considered a major factor affecting the distribution and abundance of submerged macrophytes, and some parameters can alter light availability, for example, fine particles, dissolved inorganic nitrogen and phosphorous, epiphytic biomass, and suspended chlorophylls (Koch 2001). Gradients of turbidity and transparency in lentic ecosystems and shading by a riparian canopy in lotic ecosystems are crucial predictors of distribution and abundance of submerged macrophytes (Mackay et al. 2003, Lacoul and Freedman 2006). Although submerged macrophytes productivity is limited by availability of phosphorous and nitrogen (Lacoul and Freedman 2006), it is more affected by water transparency rather than by the phosphorous concentration (Lehmann and Lachavanne 1999).

In general, submerged macrophytes have a wide tolerance for water temperature, and can survive at low temperature; for example, *Myriophyllum spicatum* and *Hydrilla verticillata* seeds germinate at 15°C (Hartleb et al. 1993, Rybicki and Carter 2002, Lacoul and Freedman 2006) and *Potamogeton crispus* germinates at 16°C (Jian et al. 2003). Higher temperature positively influences vegetative propagation

by promoting fragmentation of the monoecious biotype (Lacoul and Freedman 2006) and the extent of macrophyte colonization (Duarte and Kalff 1987). However, high water temperature combined with deteriorated water quality can adversely affect chemical reaction kinetics (Whitehead et al. 2009) and generally increases water column turbidity (Rooney and Kalff 2000). Accordingly, high water temperature can impede submerged macrophytes growth by limiting light availability.

A number of factors affect composition of submerged macrophytes in river ecosystems. Species composition of submerged macrophytes in a lentic environment is related to not only water chemistry but also topography, flooding, scouring, water level, substratum composition, and interactions with other biota (Bunn and Arthington 2002, Takamura et al. 2003). For example, if water level and hydrological events are relatively stable, submerged macrophytes in the littoral zone tend to stabilize with low species richness and diversity because of strong competition under stable conditions (Lacoul and Freedman 2006). Even when the chemical requirements for submerged macrophytes are met, biological, physical, geological and geochemical parameters should also be considered as factors affecting establishment and development of submerged macrophytes (Koch 2001). Climate change and future land use also affect river water quality; for example, total suspended solids and phosphorus concentration are predicted to be higher under the climate change scenario (Wilson and Weng 2011). River flows and dilution of water contaminants could be affected by projected changes in air temperature and rainfall (Whitehead et al. 2009). Earlier growing seasons, which are predicted under climate change, would result in greater productivity and wider distribution of submerged macrophytes, thereby modifying the community structures and functions in temperate freshwater ecosystems (Rooney and Kalff 2000).

Optimal management for river ecosystems requires basic information on spatial distribution of submerged macrophytes and environmental factors. Despite the lack of long-term data for submerged macrophytes, information on the distribution of submerged plants of post-regulation is potentially valuable for the conservation of aquatic habitats. The cumulative data should enable informed conclusions to be made about changes in vegetation and environmental conditions in river ecosystems because many of dominant species revealed in this study are cosmopolitan aquatic plants with a wide climatic range.

Chapter 3. The relationships between submerged macrophyte diversity and environmental factors

3.1. Introduction

A submerged macrophyte community consists of plants growing together in a particular location that have similar environmental requirements; however, different submerged macrophyte communities may have different habitat requirements, which include stream size, water chemistry, water velocity, and substratum type (Riis et al. 2000). Submerged macrophyte communities are variable in composition and, as water transparency decreases, can change from submerged plants (e.g., *Chara* spp.), to canopy producing submerged plants (e.g., *Potamogeton* spp.), to floating-leaved plants (e.g., *Trapa* spp.), and to emergent plants (e.g., *Typha* spp.) (Chambers 1987, Egertson et al. 2004). With this shift in communities, abundance and diversity of submerged macrophytes typically decrease (Egertson et al. 2004). Curves fit to species-abundance distributions are used to evaluate community maintenance, analyze community structure, and infer community properties (Connolly and Thibaut 2012).

Disturbance and productivity are primary factors that regulate species richness in plant communities (Pollock et al. 1998). Huston (1979) proposed that species richness will be highest at intermediate levels of disturbance and productivity-stress. According to this theory, the most tolerant species can live under extreme stress and disturbance, whereas the most competitive species adapt to minimal stress and high productivity (Makkay et al. 2008). At intermediate levels of disturbance/productivity, both competitive and disturbance-tolerant species co-exist (Arthaud et al. 2013). The recent reductions in biodiversity have generated both scientific and political interest, largely as a result of the dramatic effects caused by human-induced changes in ecosystems (Lopatin et al. 2016). The diversity of submerged macrophyte

communities has been studied in relation to factors correlated with disturbance, such as flood frequency (Riis and Biggs 2003), water level fluctuation (Riis and Hawes 2002), boat traffic (Buchan and Padilla 2000), and water velocity (Nilsson 1987), and in relation to factors correlated with productivity and stress, such as nutrient concentrations (Rolon and Maltchik 2006), light availability (Bolpagni et al. 2016), and standing crop (Makkay et al. 2008).

In addition to disturbance and productivity, diversity is also strongly influenced by spatial heterogeneity (Pollock et al. 1998). Environmental heterogeneity includes local environmental factors at small spatial scales, which can affect plant composition and diversity (Paudel and Vetaas 2014) by providing a high diversity of niches (Lopatin et al. 2016). The diversity and richness of submerged macrophyte communities are closely correlated with aspects of environmental heterogeneity that include the shade of riparian trees (Gee et al. 1997), water transparency (Vestergaard and Sand-Jensen 2000), water trophic state (Toivonen and Huttunen 1995), substratum composition (Baatrup-Pedersen and Riis 1999), landscape features (Cheruvilil and Soranno 2008), wave exposure (Koch 2001), and spatial scale (Ranieri et al. 2015).

The essential roles of submerged macrophytes in rivers are primary production and providing shelters for aquatic organisms (Rolon and Maltchik 2006). However, by forming dense beds, submerged macrophytes also negatively affect the diversity, impede water flow, and reduce the open area in littoral zones (Buchan and Padilla 2000). An understanding of the mechanisms for changes in the submerged macrophyte community and the relationships between diversity and the local environment is an essential step for river ecosystem management and suitable ecosystem quality assessments (Chappuis et al. 2014). Additionally, to develop

appropriate strategies for conservation and management for submerged macrophytes, identifying and monitoring species richness is necessary (Turner et al. 2003, Lopatin et al. 2016). In Korea, the structure of submerged macrophyte communities remains unexplored, and the influence of environmental factors on submerged macrophyte diversity has yet to be surveyed comprehensively.

In the present study, an extensive area of the major rivers and tributaries in Korea, covering wide gradients of water velocity and water chemistry, was examined. The primary goal of this study was to determine the short-term changes in submerged macrophytes communities and water column conditions. Additionally, the environmental gradient factors that significantly influenced submerged macrophytes community structure and diversity were identified.

3.2. Methods

3.2.1. Study area

A total of 197 sites were selected and studied during two growing seasons (from May to September in 2014 and 2015) in rivers and tributaries in Korea (33°–39° N, 124°–130° E). Among these sites, two sites were used for short-term monitoring for three years (summer season, from 2014 to 2016), which were in Han River (37°29.1' N, 127°29.3' E; Yangpyeong site) and Nakdong River (36°24.7' N, 128°14.8' E; Sangju site) (Fig. 3-1). These monitoring sites were located close to the large-scale weirs and expected to have noticeable changes in submerged macrophytes.

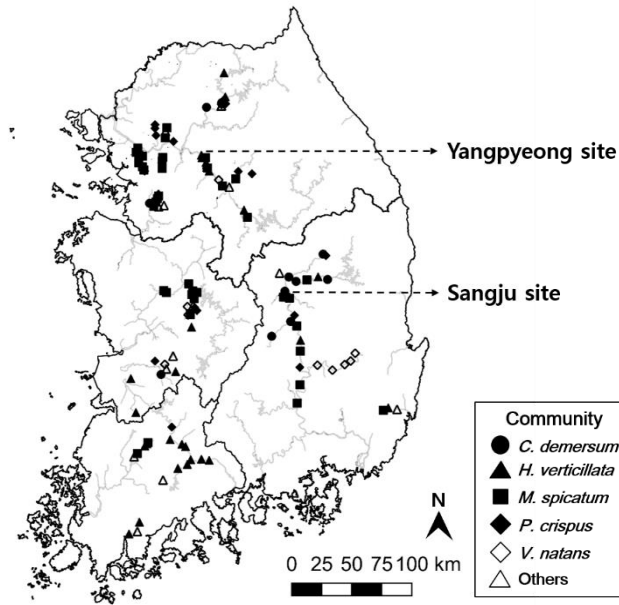


Fig. 3-1. Locations of classified submerged macrophyte communities at 128 vegetated sites of submerged macrophytes at the Korean streams. ● *C. de*, *Ceratophyllum demersum* community; ▲ *H. ve*, *Hydrilla verticillata* community; ■ *M. sp*, *Myriophyllum spicatum* community; ◆ *P. cr*, *Potamogeton crispus* community; ◇ *V. na*, *Vallisneria natans* community; △ Others, the others community. The three-year monitoring sites, Yangpyeong site in Han River (37°29.1' N, 127°29.3' E) and Sangju site in Nakdong River (36°24.7' N, 128°14.8' E).

3.2.2. Data collection

Vegetation was investigated using a belt transect (50×2 m) along the river flow (Dawson et al. 1999, Riis et al. 2001). At each site, species were observed directly from the water surface, with sampling with a rake for confirmation (Gurnell et al. 2010), or sometimes from a boat. Species and percent coverage were recorded for a total of 128 vegetated sites among the 197 sites. The remaining 69 sites did not contain submerged macrophytes and were not included in the current analysis.

Studied sites were assigned to water quality monitoring towers to obtain water quality data from the Ministry of Environment's national water quality measurement network (<http://water.nier.go.kr>); the data were from January 2012 to October 2015 and averaged monthly. Water chemical parameters, including BOD, chlorophyll *a*, ammonium nitrogen, nitrate nitrogen, suspended solids, total nitrogen, total dissolved phosphorous, total organic carbon, and total phosphorus are known to be important submerged macrophytes. Water quality data of the Yangpyeong and Sangju monitoring sites were acquired from January 2012 to September 2016. Because Sangju site was not exactly assigned to a water quality monitoring tower, I obtained water quality data of Sangju site from two monitoring towers; upstream ("Donam" water monitoring tower) and downstream ("Sangju2" water monitoring tower). In Chapter 2, I described the details of the methods of data collection for water depth and water velocity. Representative substratum types in each transect were recorded and categorized as boulder (> 256 mm diameter), cobble (64–256 mm), pebble (16–64 mm), and fines (< 16 mm) (Gurnell et al. 2010). The primary chemical and physical parameters of the water column at the 128 vegetated sites are shown in Table 3-1.

Table 3-1. Descriptive statistics for chemical and physical variables of 128 vegetated sites. Biochemical oxygen demand, chlorophyll *a*, ammonium nitrogen, nitrate nitrogen, suspended solids, total dissolved phosphorus, total nitrogen, total organic carbon, and total phosphorus were presented as means \pm standard errors of monthly measurements from 2012 to 2015. Water temperature was calculated for the growing season (from May to October), and the representative substratum type, water depth, and water velocity were measured on the sample date

Variable	Mean \pm SE	Range
Biochemical oxygen demand [mg L ⁻¹]	2.2 \pm 0.2	0.6–14.3
Chlorophyll <i>a</i> [mg m ⁻³]	10.7 \pm 0.7	2.1–45.4
Ammonium nitrogen [mg L ⁻¹]	0.70 \pm 0.14	0.03–8.23
Nitrate nitrogen [mg L ⁻¹]	2.26 \pm 0.09	0.51–5.88
Suspended solids [mg L ⁻¹]	7.7 \pm 0.4	1.2–31.6
Total dissolved phosphorus [mg L ⁻¹]	0.07 \pm 0.01	0.01–1.26
Total nitrogen [mg L ⁻¹]	3.78 \pm 0.24	0.91–15.05
Total organic carbon [mg L ⁻¹]	3.12 \pm 0.14	0.94–11.77
Total phosphorus [mg L ⁻¹]	0.10 \pm 0.01	0.02–1.51
Water temperature [°C]	22.8 \pm 0.2	17.7–25.5
Water depth [m]	0.61 \pm 0.03	0.15–1.60
Water velocity [m s ⁻¹]	0.09 \pm 0.01	0.00–0.90
Representative substratum type		
Fines (< 16 mm)	51 sites	
Pebble (16–64 mm)	26 sites	
Cobble (64–256 mm)	33 sites	
Boulder (> 256 mm)	18 sites	

3.2.3. Diversity index and water quality changes

Studied sites were grouped into five representative communities based on the most abundant species (Riis et al. 2000). Fewer than ten sites were grouped into a community characterized as “others”. When two dominant species had the identical cover at a given site, the site was classified into the community with fewer total numbers to balance the numbers among communities. The diversity indices were species richness and the Shannon diversity index. For each site, the importance value for each species was calculated (importance value = relative cover + relative frequency) (Schlising and Sanders 1982) and the species richness was determined as the number of species for submerged macrophytes (Angeler and Drakare 2013). The Shannon diversity index was also determined (McClanahan 1986). The changes in water quality for five years were represented at the two monitoring sites (Yangpyeong and Sangju sites) using “ggplot2” package (Wickham 2009); BOD, chlorophyll *a*, ammonium nitrogen, nitrate nitrogen, suspended solids, total nitrogen, total organic carbon, and total phosphorus.

3.2.4. Environmental factors influencing the submerged macrophyte community

Statistical analyses were performed using the R statistical software package (R Development Core Team 2016), with significance levels either significant ($p < 0.05$) or nonsignificant ($p > 0.05$) (Zhang et al. 2016). Before analyses, the covariation among the environmental variables was tested using Pearson correlation analysis (Rolon and Maltchik 2006) (Table 3-2). The variables with a correlation coefficient greater than 0.75 were excluded to eliminate interference from multicollinearity

(Kuhn and Johnson 2013). Ultimately, five water chemicals (chlorophyll *a*, ammonium nitrogen, nitrate nitrogen, suspended solids, total phosphorous) were selected and included in all analyses. In addition, representative substratum type, water depth, and water velocity were included in analyses.

Mean diversity indices were compared among communities using Mann-Whitney *U* tests because of different variances and sample sizes (Cardinale et al. 2002). Canonical correspondence analysis (CCA) was used to determine correlations between submerged macrophyte communities and environment variables. The CCA is a multivariate constrained ordination which extracts the primary environmental gradients within the community composition using abundance data (Bergfur and Sundberg 2014). Stepwise selection using 999 Monte Carlo permutations was run to determine the significant variables that best described the gradients in submerged macrophyte communities (Tererai et al. 2013, Bergfur and Sundberg 2014).

3.2.5. Environmental factors related to submerged macrophyte diversity

To examine the differences between submerged macrophyte diversity in the communities, I used Kruskal-Wallis non-parametric one-way analysis of variance (Kemp et al. 1990). When the differences in submerged macrophyte diversity (Shannon diversity index and species richness) between the communities were statistically significant from Kruskal-Wallis test, post-hoc testing with the Mann-Whitney *U* test demonstrated differences in diversity indices (Coccia et al. 2016).

Generalized linear models (GLMs) were used, extending nonlinearity and nonconstant variance structures in the data (Guisan et al. 2002), to identify the

significant environmental variables affecting diversity indices across all 128 sites. Shannon diversity index and species richness, assumed as normal and Poisson distributions, respectively, were delineated along the primary environmental factors resulting from the GLMs. Five water chemicals (chlorophyll *a*, ammonium nitrogen, nitrate nitrogen, suspended solids, total phosphorous) were selected and included in GLM analyses. In addition abiotic factors, water depth and water velocity, were included in analyses.

Table 3-2. Pearson correlation coefficients for nine water chemical variables.

Bold text indicates significant correlations ($p < 0.05$)

	BOD	Chla	NH4N	NO3N	SS	TDP	TN	TOC	TP
BOD	1.00								
Chla	0.46	1.00							
NH4N	0.78	0.14	1.00						
NO3N	0.48	0.34	0.44	1.00					
SS	0.65	0.67	0.32	0.34	1.00				
TDP	0.86	0.32	0.59	0.30	0.61	1.00			
TN	0.80	0.29	0.90	0.77	0.41	0.59	1.00		
TOC	0.92	0.54	0.76	0.52	0.69	0.77	0.80	1.00	
TP	0.87	0.35	0.61	0.33	0.65	0.99	0.61	0.79	1.00

Note: BOD, biochemical oxygen demand; Chla, chlorophyll *a*; NH4N, ammonium nitrogen; NO3N, nitrate nitrogen; SS, suspended solids; TDP, total dissolved phosphorus; TN, total nitrogen; TOC, total organic carbon; TP, total phosphorus.

3.3. Results

3.3.1. Changes in importance values of submerged macrophytes and water column conditions

The changes in the importance values of the submerged macrophyte species at the monitoring sites are shown in Figure 3-2. In the first year at the Yangpyeong site in the Han River, *Hydrilla verticillata* and *Vallisneria natans* were the most important species; however, the importance values of these species decreased in the following years. The importance of *Najas marina* and *Potamogeton malaianus* increased sharply, and these species became predominant in the Yangpyeong site. At the Sangju site in the Nakdong River, *Myriophyllum spicatum* was only found in the first year; however, other species, such as *H. verticillata* and *N. marina*, became widely distributed and important species.

The site-specific observations showed different trends and large fluctuations in the environmental variables at the two sites (Figs. 3-3 and 3-4). At Yangpyeong site from 2012 to 2016, BOD, chlorophyll *a*, and total organic carbon increased whereas ammonium nitrogen, nitrate nitrogen, suspended solids, total nitrogen and total phosphorus decreased (Fig. 3-3). At the Sangju site, BOD, chlorophyll *a*, total nitrogen, and total organic carbon tended to increase; however, total phosphorus decreased from 2012 to 2016 (Fig. 3-4). No changes in ammonium nitrogen, nitrate nitrogen, and suspended solids were observed at the Sangju site.

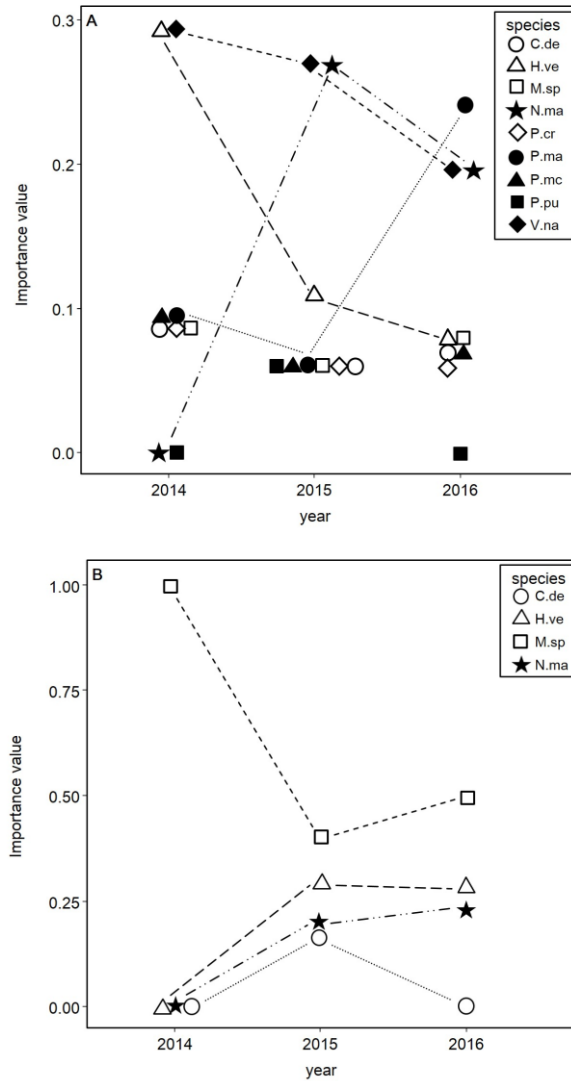


Fig. 3-2. Changes in importance values of submerged macrophytes for three years at the (A) Yangpyeong site in the Han River and (B) Sangju site in the Nakdong River. ○ C.de, *Ceratophyllum demersum*; △ H.ve, *Hydrilla verticillata*; □ M.sp, *Myriophyllum spicatum*; ★ N.ma, *Najas marina*; ◇ P.cr, *Potamogeton crispus*; ● P.ma, *P. malaianus*; ▲ P.mc, *P. maackianus*; ■ P.pu, *P. pusillus*; ◆ V.na, *Vallisneria natans*.

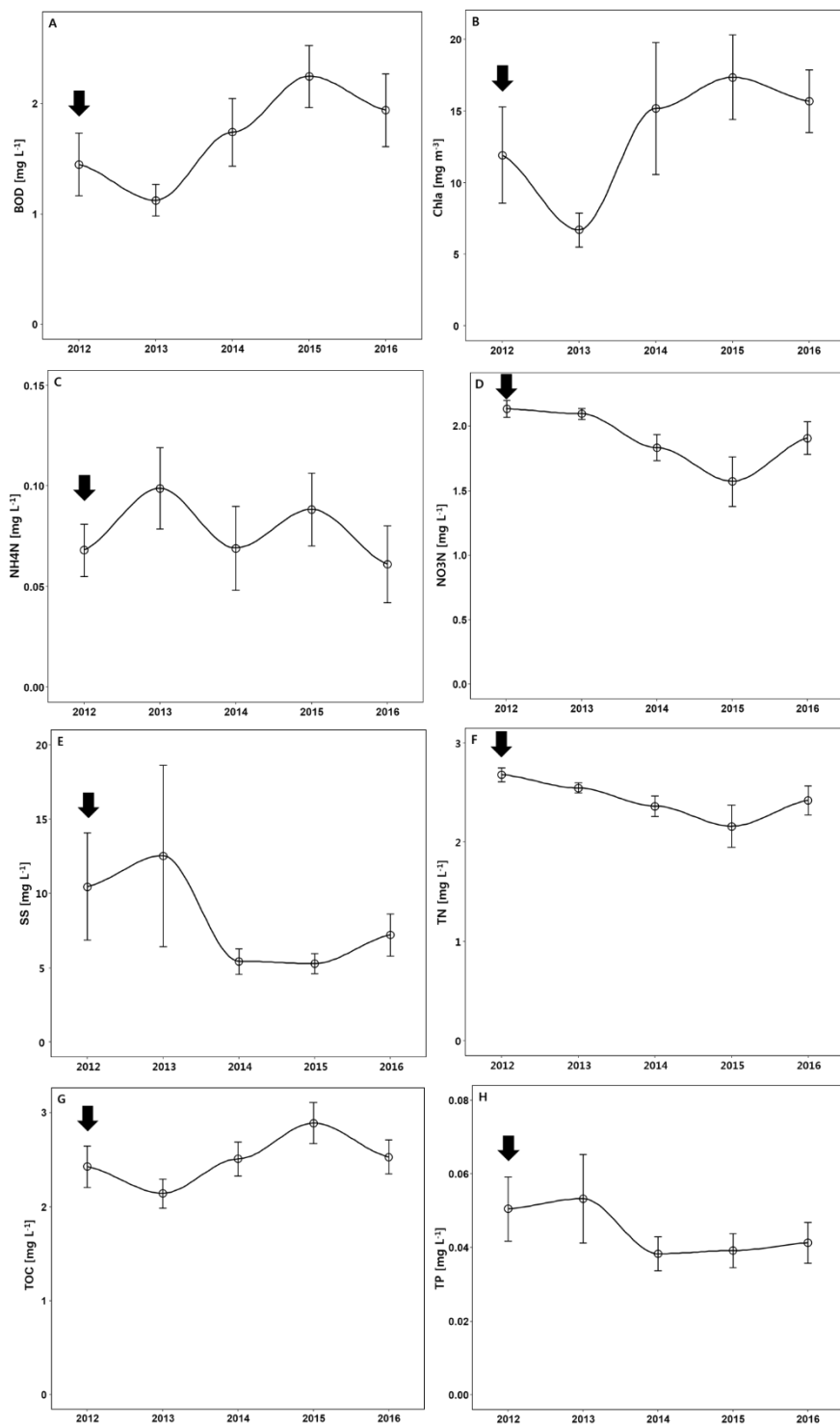


Fig. 3-3. Changes in water quality for eight variables (mean \pm standard error) between 2012 and 2016 at the Yangpyeong site in the Han River. (A) BOD, biochemical oxygen demand; (B) Chla, chlorophyll *a*; (C) NH₄N, ammonium nitrogen; (D) NO₃N, nitrate nitrogen; (E) SS, suspended solids; (F) TN, total nitrogen; (G) TOC, total organic carbon; and (H) TP, total phosphorus. Arrows in each figure represent the end period of the weir construction. Bold lines indicate fitted values to the data for each variable versus year using “ggplot2” package.

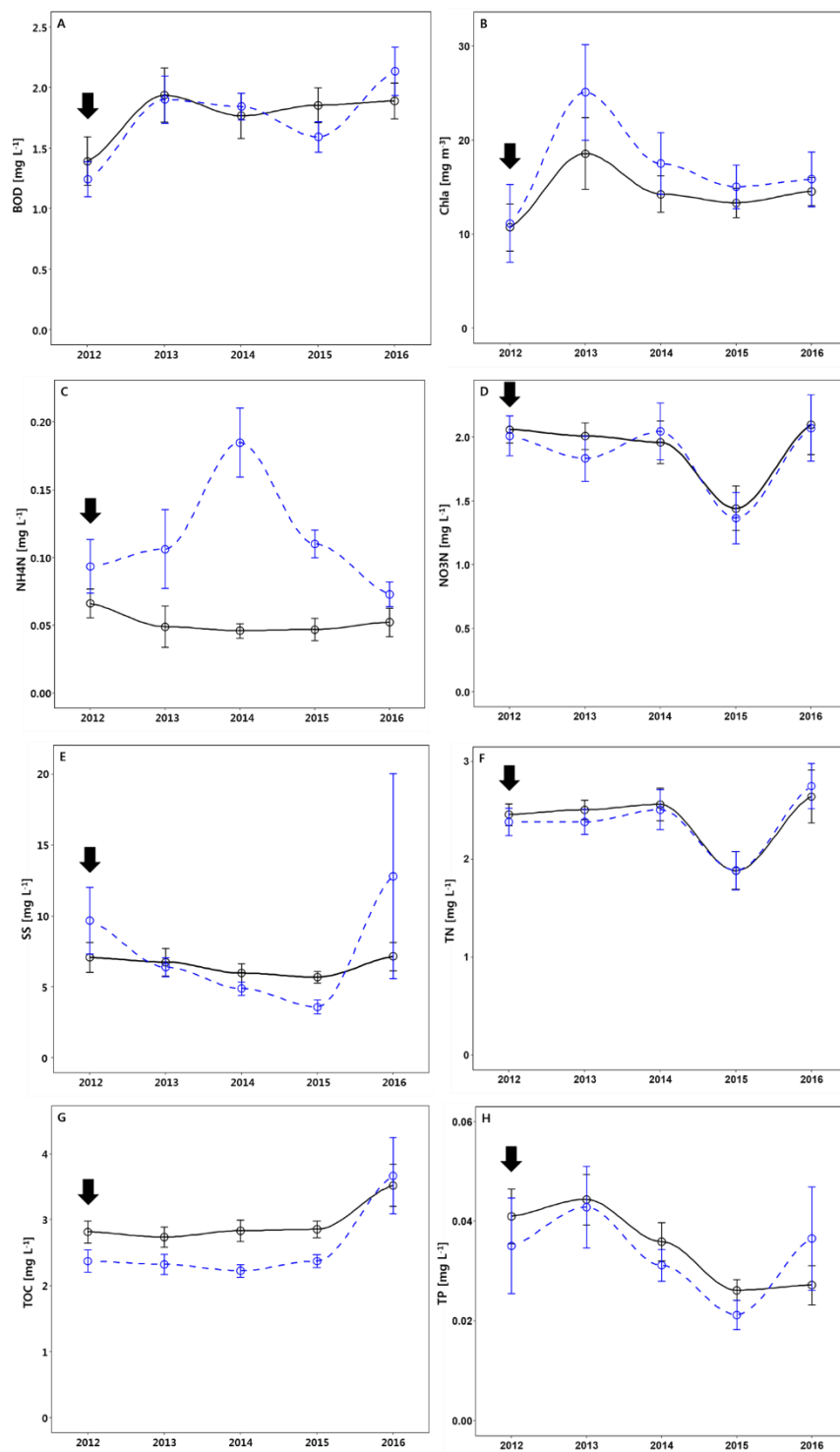


Fig. 3-4. Changes in water quality for eight variables (mean \pm standard error) between 2012 and 2016 at the Sangju site in the Nakdong River. (A) BOD, biochemical oxygen demand; (B) Chla, chlorophyll *a*; (C) NH₄N, ammonium nitrogen; (D) NO₃N, nitrate nitrogen; (E) SS, suspended solids; (F) TN, total nitrogen; (G) TOC, total organic carbon; and (H) TP, total phosphorus. Black symbols, upstream water monitoring tower; blue symbols, downstream water monitoring tower. Arrows in each figure represent the end period of the weir construction. Bold lines indicate fitted values to the data for each variable versus year using “ggplot2” package.

3.3.2. Multiple factors affecting submerged macrophyte community

Based on the CCA ordination, nitrate nitrogen, total phosphorus and water depth were significant influences on the communities ($p < 0.05$) (Fig. 3-5). The first two axes of the CCA ordination explained 75% of the variance of the community-environment relationship. Standard deviation ellipses were depicted for the communities on a biplot, which showed that the first axis was correlated with nitrate nitrogen, with increasing nutrient concentration from left to right. The *Potamogeton crispus* and *Myriophyllum spicatum* communities were most affected by a high concentration of nitrate nitrogen, whereas the *Hydrilla verticillata* community was found when nitrate nitrogen parameters were in low concentration. The second axis was correlated with total phosphorus and water depth. *Vallisneria natans* community was associated with deeper water depth. *Ceratophyllum demersum* community and *P. crispus* community were correlated with higher total phosphorus concentration.

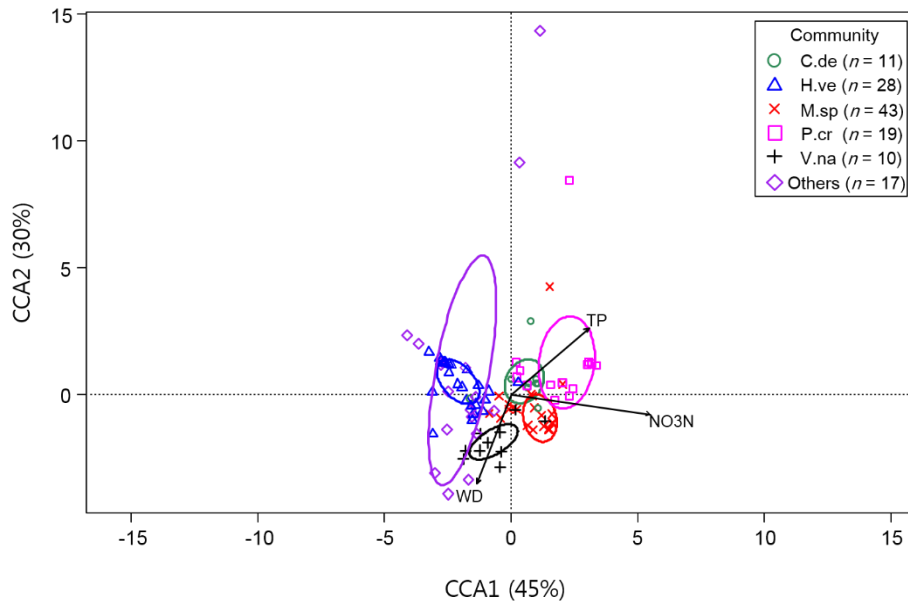


Fig. 3-5. Biplot of canonical correspondence analysis (CCA) ordination of 128 sites that were classified into submerged macrophyte communities. The ordination was constrained on significant factors with arrows; nitrate nitrogen (NO₃N), total phosphorus (TP), and water depth (WD) ($p < 0.05$). The six ellipses represent submerged macrophytes community based on the standard deviations: ○, *Ceratophyllum demersum* community; △, *Hydrilla verticillata* community; ×, *Myriophyllum spicatum* community; □, *Potamogeton crispus* community; +, *Vallisneria natans* community; ◇, others community.

3.3.3. Submerged macrophyte diversity and response to environmental factors

The diversity indices of the different communities are compared in Figure 3-6. The Shannon diversity index and species richness showed the same pattern; the highest index of diversity was for the *Vallisneria natans* community, followed by the others community and then *Hydrilla verticillata*, *Ceratophyllum demersum*, *Potamogeton crispus*, and *Myriophyllum spicatum* communities.

Based on a GLM, the significant variables for Shannon diversity index and species richness were ammonium nitrogen, nitrate nitrogen, and water velocity (Table 3-3). According to GLMs, the diversity indices response curves to ammonium nitrogen, nitrate nitrogen, and water velocity (Figs. 3-7 and 3-8) were monotonously negative relationships. The highest Shannon diversity index and species richness were found in waters with a low concentration of ammonium nitrogen and nitrate nitrogen, and slow water flow.

Table 3-3. Environmental variables related to the Shannon diversity index and species richness by generalized linear models (GLMs). Based on GLMs, the significant variables related to Shannon diversity index and species richness were ammonium nitrogen, nitrate nitrogen, and water velocity. The significant variables were selected using t -value for Shannon diversity index and z -value for species richness with p to enter/leave = 0.05

Selected variables	α Coefficient	β Coefficient	t -value (z -value)	p -value
(a) Shannon diversity index				
$\mu(\text{Shannon index}) = f(\alpha + \beta \text{ NH}_4\text{N})$	0.88	-0.10	-2.88	0.005
$\mu(\text{Shannon index}) = f(\alpha + \beta \text{ NO}_3\text{N})$	1.17	-0.16	-2.98	0.003
$\mu(\text{Shannon index}) = f(\alpha + \beta \text{ WV})$	0.91	-1.05	-3.05	0.003
(b) Species richness				
$\mu(\text{richness}) = f(\alpha + \beta \text{ NH}_4\text{N})$	1.14	-0.13	-2.85	0.004
$\mu(\text{richness}) = f(\alpha + \beta \text{ NO}_3\text{N})$	1.48	-0.19	-3.25	0.001
$\mu(\text{richness}) = f(\alpha + \beta \text{ WV})$	1.16	-1.20	-2.81	0.005

Note: NH₄N, ammonium nitrogen; NO₃N, nitrate nitrogen; WV, water velocity.

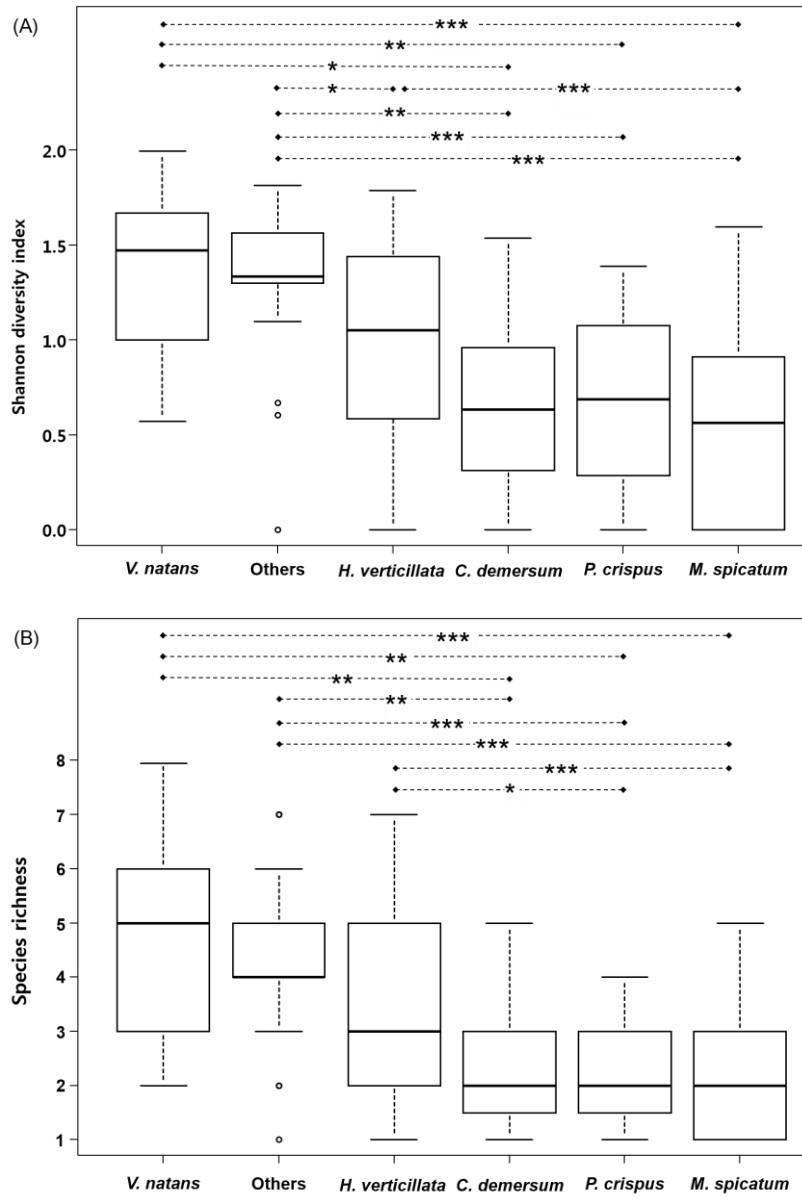


Fig. 3-6. Comparison of (A) Shannon diversity index and (B) species richness of submerged macrophyte communities. *Ceratophyllum demersum* community, $n = 11$; *Hydrilla verticillata* community, $n = 28$; *Myriophyllum spicatum* community, $n = 43$; *Potamogeton crispus* community, $n = 19$; *Vallisneria natans* community, $n = 10$; and others community, $n = 17$. Boxplots encompass the 25% and 75% quartiles; the central solid lines represent the median. Whiskers represent the minimum and maximum values; open circles identify outliers. Significant differences in diversity indices among communities were determined by the Mann-Whitney U test. Significance levels are indicated as follows: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

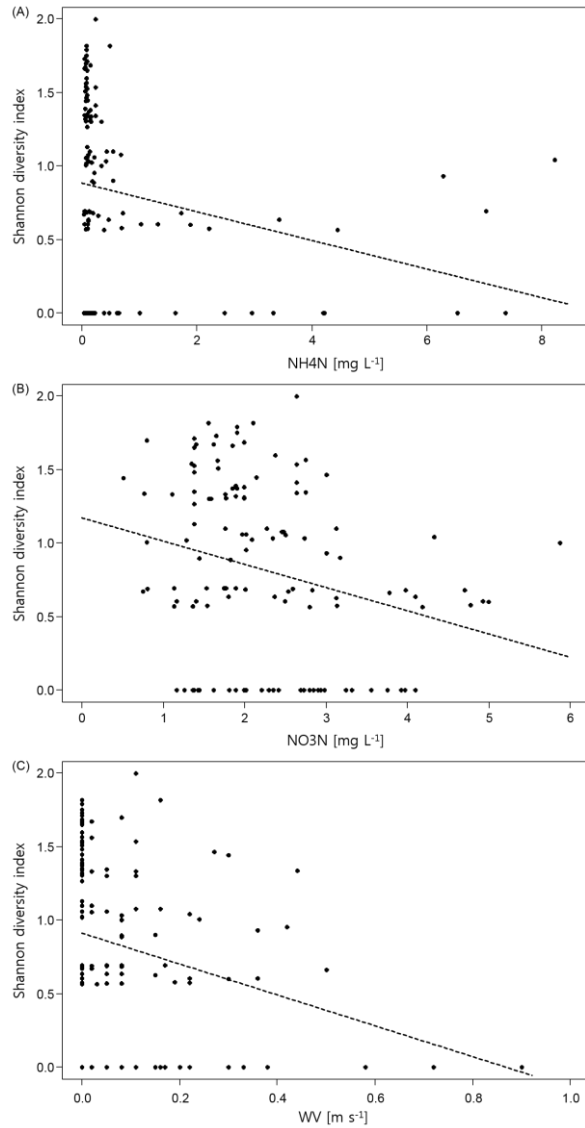


Fig. 3-7. Relationships between Shannon diversity index and environmental factors. Shannon diversity index of submerged macrophyte communities on the gradient of (A) ammonium nitrogen (NH₄N), (B) nitrate nitrogen (NO₃N), and (C) water velocity (WV) were modeled with generalized linear models (GLMs). Dots represent individual sites.

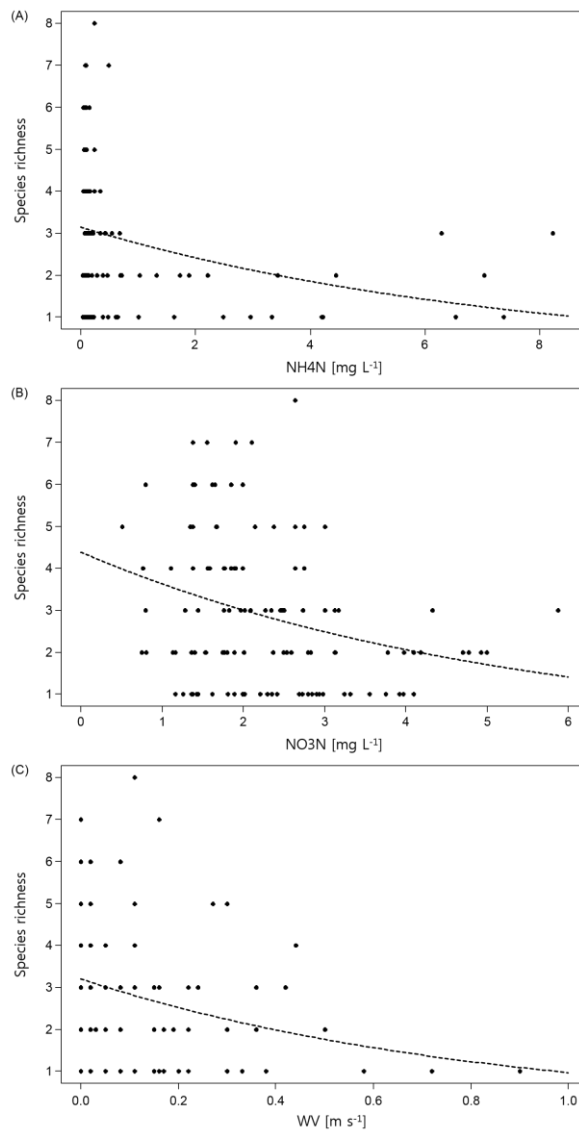


Fig. 3-8. Relationships between species richness and environmental factors.

Species richness of submerged macrophyte communities on the gradient of (A) ammonium nitrogen (NH₄N), (B) nitrate nitrogen (NO₃N), and (C) water velocity (WV) were modeled with generalized linear models (GLMs). Dots represent individual sites.

3.4. Discussion

3.4.1. Establishment and expansion of *Najas marina*

In this study, *Najas marina* became widely distributed within a few years and was the only annual plant at the Yangpyeong and Sangju sites. The unique phenomena of the *N. marina* expansion might be attributed to the coarse, spine-tipped teeth and thick cuticle on the leaves, which are a physical defense against fish grazing (Qiu et al. 2001). According to Olivera-Gomez and Mellink (2013), *N. marina* is a fragile annual and is easily detached from the sediment, thus this species has low competitive ability (Pedro et al. 2006). However, Handley and Davy (2002) found that *N. marina* develops extensive root systems. In addition, this species is categorized as a pioneer species and *r*-strategist, which can survive in unfavorable habitats and easily increase in more favorable habitats (Dong-ru et al. 1997). *Najas marina* is sometimes regarded as a perennial because of the turions, which are dormant for long periods and carry vegetative buds (Agami et al. 1986). Seeds of *N. marina* have a relatively large mass (ca. 5 mg) as an adaptation to burial (Handley and Davy 2002) and germinate well in limited light conditions because of a low light compensation point (Dong-ru et al. 1997). Although confirmation of competitive relationships between submerged macrophytes is difficult, a mutual inhibitory effect is likely between *Myriophyllum spicatum* and *N. marina* in the competition for common resources (Agami and Waisel 2002). In summary, *N. marina* is well adapted for widespread establishment because of these advantageous characteristics.

3.4.2. Submerged macrophyte diversity and response to environmental gradients

Vallisneria natans community had relatively even distribution of species and high Shannon diversity index and species richness. Despite occurring the most frequently ($n = 43$), the *Myriophyllum spicatum* community had the lowest diversity indices among the communities, because this species was widely found with only a few other species or as the only species. The CCA ordination identified the environmental gradient factors significantly affecting community distributions were nitrate nitrogen, total phosphorus, and water depth.

The GLM identified ammonium nitrogen, nitrate nitrogen and water velocity as the significant variables for modeling the Shannon diversity index and species richness, which were negatively correlated with these environmental variables. The same pattern of nitrate nitrogen has been reported by Hrivnák et al. (2014); species richness had a negative relationship with nitrate nitrogen concentration. This result was not exactly consistent with that of other studies, because the relationship between the submerged macrophytes richness and water trophy is hump-shaped, with the maximum richness in a mesotrophic condition (Rørslett 1991, Vestergaard and Sand-Jensen 2000). Although nutrients lead the growth and distribution of submerged macrophytes, nutrient enrichment can inhibit growth (Demars and Harper 1998, Michael Kemp et al. 2004). Therefore, eutrophication of shallow freshwaters is one cause leading to the disappearance of submerged macrophytes (Körner 2002) and low diversity.

Consistent with the results of Makkay et al. (2008), water velocity had a negative influence on species diversity. Moreover, Chambers et al. (1991) also

reported that aquatic macrophyte biomass was inversely correlated with water velocity. Water flow is a crucial determinant of the physical habitat and the biotic composition of submerged macrophytes (Bunn and Arthington 2002), and current velocity serves as natural physical disturbance to aquatic assemblages (Nilsson 1987). High water velocity causes the erosion of sediments and inhibits the growth of submerged macrophytes (Sand-Jensen and Vindbæk Madsen 1992, Riis et al. 2000). Once established, both the abundance and diversity of submerged macrophytes are stimulated at low to medium water flow (Janauer et al. 2010). Moreover, the distribution of submerged macrophytes is both the cause and the effect of environmental conditions such as water flow (Janauer et al. 2010, Chappuis et al. 2014). Submerged macrophytes is usually distributed in dense patches, which reduce the water velocity and the probability of uprooting (Sand-Jensen and Vindbæk Madsen 1992). Reciprocally, the proliferation of dense patches also leads to shading among neighbors, which reduces photosynthesis, retards growth, and lowers submerged macrophyte diversity (Sand-Jensen and Vindbæk Madsen 1992, Buchan and Padilla 2000). In summary, in order to maintain submerged macrophyte diversity, an understanding of the mutual relationship between submerged macrophytes and water flow is required.

More investigations of the community structure and submerged macrophyte diversity are required for optimal management of river ecosystems, because submerged macrophytes alter the water quality (Zhang et al. 2016) and habitats for other biota such as fish, invertebrates, and periphyton (Riis and Biggs 2003). Water environmental conditions and submerged macrophyte community structure should be monitored together in the long-term, because both can change rapidly within a few years and the relation is complicated with reciprocal effects.

**Chapter 4. Potential habitat environment of two
submerged macrophytes, *Myriophyllum
spicatum* and *Hydrilla verticillata***

4.1. Introduction

Submerged macrophytes play an important role as a producer in the food web, shelter and forage for other organisms, and a water quality indicator (Nieder et al. 2004). In addition, submerged macrophytes produce oxygen in stagnant regions and prolong the hydrologic retention time for the removal of particulate nutrients (Nepf et al. 2007). Despite the importance of submerged macrophytes, the formation of dense monotypic stands has adverse effects on the diversity and richness of invertebrates and fish (Buchan and Padilla 2000). Dense submerged macrophytes can produce organic materials from actively growing or senescing macrophytes and cause eutrophication of the water column (Chambers et al. 1999). Moreover, their proliferation can impede water flow, clog the inlets of reservoirs, and interfere with recreational activities (Kenneth 1996).

The spatial distribution of organisms is related to species dispersal and survival at a regional scale. In addition, abiotic conditions (environmental constraints) and biotic interactions (e.g., competition and herbivory) influence species distributions at a local scale (Austin 2002, Bučas et al. 2013, Chappuis et al. 2014). The occurrence and abundance of submerged macrophytes are influenced by chemical and physical factors, such as water quality, light availability (Dennison et al. 1993), water transparency, water depth (Canfield et al. 1985), channel slope, channel dimensions (O'Hare et al. 2011), and hydrological regime (Franklin et al. 2008). Understanding how diverse environmental factors affect the habitats of submerged macrophytes is important for flow control, sediment transport (Järvelä 2005), and assessments of the ecological condition of rivers (Clayton and Edwards 2006).

A variety of statistical approaches such as generalized linear models and

generalized additive models (GAMs) are important tools for predicting the likely occurrence or distribution of a species (Pearce and Ferrier 2000, Austin 2002). In particular, GAMs are used extensively in habitat suitability modeling and identification of the optimal environmental conditions for a given species; data are fitted using a semi-parametric model to predict non-linear responses to the exploratory variables (Elith et al. 2006, Drexler and Ainsworth 2013, Li and Wang 2013). GAMs not only have a strong statistical foundation, but can be used to realistically model ecological relationships (Yee and Mitchell 1991, Sanchez et al. 2008). When the relationship between a species distribution and environmental variables is complex, GAMs are practical and perform as well or better than other types of predictive models (Drexler and Ainsworth 2013, Li and Wang 2013). GAMs have been used to examine potential seagrass habitats (Lathrop et al. 2001, Downie et al. 2013), fish production and distributions (Borchers et al. 1997, Buisson et al. 2008, Murase et al. 2009, Solanki et al. 2016), and terrestrial plant distributions (Yee and Mitchell 1991, Austin and Meyers 1996, Thuiller et al. 2005), but few studies have used GAMs to examine submerged macrophytes in freshwater ecosystems.

Recently, river ecosystems in South Korea have experienced channel dredging, channelization, and dam construction for flood control during rainfall periods and to secure water resources during drought periods (Woo 2010). In particular, the “Four Major Rivers Project” (2009–2012) involved the construction of 16 weirs and three dams in the Han, Geum, Nakdong, and Yeongsan Rivers (Lah et al. 2015). This national project aimed to secure water resources, reduce flooding, improve water quality, and create multipurpose public spaces for local residents (Jun and Kim 2011). Despite substantial controversy surrounding the effectiveness of this project (Normile 2010), it drastically changed the natural riverine habitats and enabled the

artificial manipulation of the water level and the regulation of water flow. The modified slow velocity in regulated streams may increase the abundance of macrophytes (Bunn and Arthington 2002) and devastate habitats for organisms adapted to the natural discharge regime (Dynesius and Nilsson 1994).

Alterations to hydrological regimes affect the structure and function of aquatic ecosystems, resulting in changes in the spatial distributions of submerged macrophytes (Tian et al. 2015). Submerged macrophytes in the river ecosystems of South Korea were found to expand across slow flowing streams to large rivers after weir construction. *Myriophyllum spicatum* (Eurasian watermilfoil) and *Hydrilla verticillata* (Hydrilla) are native species in South Korea; however, they are fast growing and most abundant in the river ecosystems. They are invasive species and strong competitors in Europe, the United States, and South America owing to their rapid and dense growth (Van et al. 1999, Gassmann et al. 2006, Beck et al. 2008). These two species are cosmopolitan angiosperms with extensive worldwide ranges (Zhou et al. 2016) and overrun various habitats, from lentic to lotic systems, and in turn affect flow velocity and nutrient cycling in the water column (Sousa 2011).

Accordingly, it is necessary to understand the current distribution and predict the potential habitats of submerged macrophytes with highly invasive potential for river management and conservation planning. Few studies have predicted the distributions of submerged macrophytes using GAMs. Moreover, the developed GAMs have rarely been validated via field verification. The aims of our study were to examine under what environmental conditions *Myriophyllum spicatum* and *Hydrilla verticillata* are likely to occur and to predict their potential habitats. Our specific objectives were (1) to characterize the relationship between environmental variables and the occurrence of two submerged macrophytes (*M. spicatum* and *H.*

verticillata) using GAMs, (2) to predict the potential habitats for these two submerged macrophytes, and (3) to evaluate GAMs by applying field data.

4.2. Materials and methods

4.2.1. Study sites and data collection

For the vegetation survey, 197 sites in the rivers and tributaries were selected, including 71 sites in the Han River, 43 sites in the Geum River, 46 sites in the Nakdong River, 27 sites in the Yeongsan River, and 10 sites in the Seomjin River. In Chapter 2 and 3, I described the details of the methods of data collection. For field verification, vegetation surveys were conducted from June to July in 2016 and water quality data were acquired from the Ministry of Environment's national water quality measurement network (<http://water.nier.go.kr>) from January 2012 to April 2016.

4.2.2. Model building

All statistical analyses were performed in R (R Development Core Team 2016). Prior to the statistical analysis, all explanatory variables were log10-transformed to improve normality (Chappuis et al. 2014). Pearson correlation analyses were performed to detect high multicollinearity, since the water chemical variables were correlated with each other (Zhao et al. 2014, Wedding and Yoklavich 2015). The variables with pairwise correlation coefficients greater than 0.75 were eliminated (Kuhn and Johnson 2013). Total nitrogen, BOD, COD, ammonium nitrogen, total phosphorus, total organic carbon, and total dissolved nitrogen were excluded because they were highly correlated with suspended solids, nitrate nitrogen, and total

dissolved phosphorus. Multivariate statistical methods, such as principal component analysis (PCA), have been recommended to determine the main environmental factors before inclusion in models (Shmueli 2010, Zhao et al. 2014). Six significant elements of water environmental factors determined via PCA were selected and two elements from in situ measurements (water depth and water velocity) were added to the GAMs. Finally, eight environmental descriptors were included in GAMs: chlorophyll *a*, electrical conductivity, nitrate nitrogen, suspended solids, total dissolved phosphorous, water temperature during the growing season, water depth, and water velocity. All variables describing the physical and chemical properties of water included in the GAMs are described in Table 4-1.

I used GAMs to approximate the probability of taxon presence with respect to the predictors. A binomial distribution was specified (presence = 1 and absence = 0) with a logit link function relating the dependent variables to the predictors. GAMs employ logistic regression to model the presence or absence at survey sites, thereby enabling the probability of species occurrence to be predicted from independent data at unsurveyed sites (Pearce and Ferrier 2000). The descriptor variables were modeled as cubic splines, with four degrees of smoothing (Lehmann 1998, Wood 2000). The most parsimonious model for each species with the fewest variables was chosen using a stepwise selection procedure (Buisson et al. 2008). To determine the best fit model, Akaike's information criterion (AIC) was used as a goodness-of-fit statistic (Zuur and Pierce 2004, Buisson et al. 2008, Sanchez et al. 2008). Models with a smaller AIC were able to explain the residual deviance better than those with a larger AIC. The best model accounted for the most variation in the data using the fewest predictors (Burnham and Anderson 1998).

Table 4-1. Mean, standard error (SE), minimum (Min), and maximum (Max) values for physical and chemical properties of water at 197 sites.

Chlorophyll *a*, electrical conductivity, total dissolved phosphorus, nitrate nitrogen, and suspended solids are presented as mean values of monthly estimates from January 2012 to October 2015, water temperature is presented as the mean from May to October, and water depth and velocity data were obtained at the sampling date

Variable	Mean	Median	SE	Min	Max
Chlorophyll <i>a</i> [mg m ⁻³]	14.0	9.6	0.9	0.9	65.1
Electrical conductivity [μS cm ⁻¹]	328	258	19	77	1515
Total dissolved phosphorus [mg L ⁻¹]	0.076	0.035	0.009	0.008	1.282
Nitrate nitrogen [mg L ⁻¹]	2.2	2.1	0.1	0.5	5.9
Suspended solids [mg L ⁻¹]	9.6	8.3	0.5	1.1	35.9
Water temperature [°C]	23.1	23.5	0.1	17.7	26.0
Water depth [m]	0.61	0.50	0.02	0.10	1.60
Water velocity [m s ⁻¹]	0.10	0.02	0.01	0.00	0.90

4.2.3. Validation of the predictive performance of models

To obtain an unbiased estimation of model performance, it is best to apply independent data that have not been used for model development (Pearce and Ferrier 2000). However, if independent data are not available, a k -fold cross-validation may be used to assess model accuracy (Pearce and Ferrier 2000, Zimmermann et al. 2007). I applied k -fold cross-validation (with $k = 10$); the data were randomly split into two datasets: 90% ($k - 1$ subsamples) was used as a training dataset to build a model and the remaining 10% (one subsample) was used as a testing dataset for validation. This procedure was repeated ten times to calculate the probabilities of occurrence, which were transformed into binary records (presence/absence) using a threshold probability (Sing et al. 2005, Araújo and Luoto 2007). To generate a confusion matrix, the Youden index was chosen as the threshold probability, which was the maximum difference between sensitivity (the probability of correct classification as positive) and specificity (the probability of correct classification as negative) (Jiménez-Valverde and Lobo 2007, Freeman and Moisen 2008), using the “SDMTools” library for model accuracy (VanDerWal et al. 2014). Coordinates of observations and predictions based on the confusion matrix were projected to World Geodetic System 84 (WGS84) using QGIS (QGIS Development Team 2016).

Model accuracy was assessed by two measures: Cohen’s kappa and the area under the receiver operating characteristic (ROC) curve (AUC) (Zimmermann et al. 2007). Cohen’s kappa is the most common method for determining the accuracy of presence-absence predictions based on a selected threshold probability, regardless of variation in prevalence (Segurado and Araujo 2004, Allouche et al. 2006). Landis and Koch (1977) suggested the following interpretation of kappa values: excellent agreement, >0.75 ; good agreement, $0.40\text{--}0.75$; and poor agreement, <0.40 . Another

method for assessing the accuracy of models uses the AUC value as a threshold-independent criterion (Fielding and Bell 1997). To construct ROC curves, all possible thresholds were used to classify the scores into confusion matrices, and the sensitivity and specificity were estimated for each matrix (Allouche et al. 2006). According to Swets (1988), AUC values were interpreted as follows: excellent, >0.90; good, 0.80–0.90; fair, 0.70–0.80; poor, 0.60–0.70; fail, 0.50–0.60. Moreover, in situ observations of the 41 sites were randomly performed to evaluate the accuracy of the model for field verification.

4.3. Results

4.3.1. GAM response curves

We applied GAMs to define the ranges of environmental factors with respect to species occurrences. The models explained 28.7% and 23.4% of the observed variation in selected variables for *Myriophyllum spicatum* and *Hydrilla verticillata*, respectively (Table 4-2). For *M. spicatum*, we found that chlorophyll *a*, nitrate nitrogen, suspended solids, water temperature, water depth, and water velocity were significant variables in the GAM. Based on the response curves, the probability of *M. spicatum* presence increased as nitrate nitrogen increased, and decreased as water temperature and suspended solids increased (Fig 4-1). The response curves for chlorophyll *a* indicated a sharp increase in the predicted presence of *M. spicatum* from 0 to ~20 mg/m³ and a decline at higher concentrations. The presence probabilities of *M. spicatum* for water velocity decreased for values of up to ~0.4 m/s and then increased in relatively rapid flows. *Myriophyllum spicatum* was

distributed in a wide range of water depths up to 1 m and decreased in deeper water. Electrical conductivity and suspended solids were important parameters determining the *H. verticillata* distribution (Table 4-2). *Hydrilla verticillata* presence was negatively related to electrical conductivity and suspended solid concentrations (Fig. 4-2). We also observed differences in the predicted potential habitats between the two species (Figs. 4-3 and 4-4). *Myriophyllum spicatum* was widely distributed in the Han River and Nakdong River, and its predicted distribution was similar to its current distribution. *Hydrilla verticillata* was abundant everywhere, whereas its distribution was predicted to be decreased in Nakdong River and increased in Yeongsan River.

Table 4-2. Selected environmental variables and deviance explained in generalized additive models (GAMs) for *Myriophyllum spicatum* and *Hydrilla verticillata*

Species	Environmental variable	Significance (<i>p</i> -value)	Deviance explained
<i>Myriophyllum spicatum</i>	Chlorophyll <i>a</i> (chl <i>a</i>)	<0.001	28.7%
	Nitrate nitrogen (NO ₃ N)	0.003	
	Suspended solids (SS)	<0.001	
	Water temperature (WT)	0.034	
	Water depth (WD)	0.030	
	Water velocity (WV)	0.010	
	<i>f</i> (occurrence) = s(chl <i>a</i>) + s(NO ₃ N) + s(SS) + s(WT) + s(WD) + s(WV), <i>k</i> =4		
<i>Hydrilla verticillata</i>	Electrical conductivity (EC)	<0.001	23.4%
	Suspended solids (SS)	0.010	
<i>f</i> (occurrence) = s(EC) + s(SS), <i>k</i> =4			

Note: *k*, degrees of smoothing of GAMs; *s*, cubic splines as smooth terms.

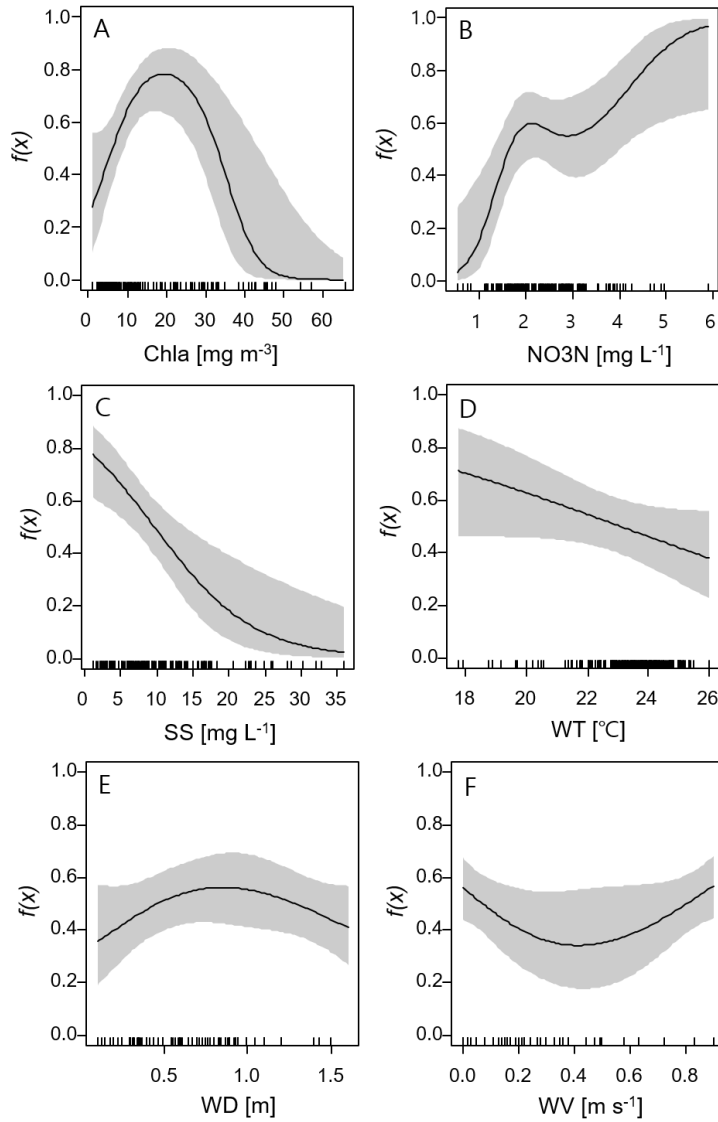


Fig. 4-1. Response curves of *Myriophyllum spicatum* for environmental gradients in generalized additive models (GAMs). The vertical axes represent the probabilities of occurrence, and shaded bands show the 95% confidence interval. Rug plots on the x-axis show data points. Chla, chlorophyll *a*; NO3N, nitrate nitrogen; SS, suspended solids; WT, water temperature during the growing season; WD, water depth; WV, water velocity.

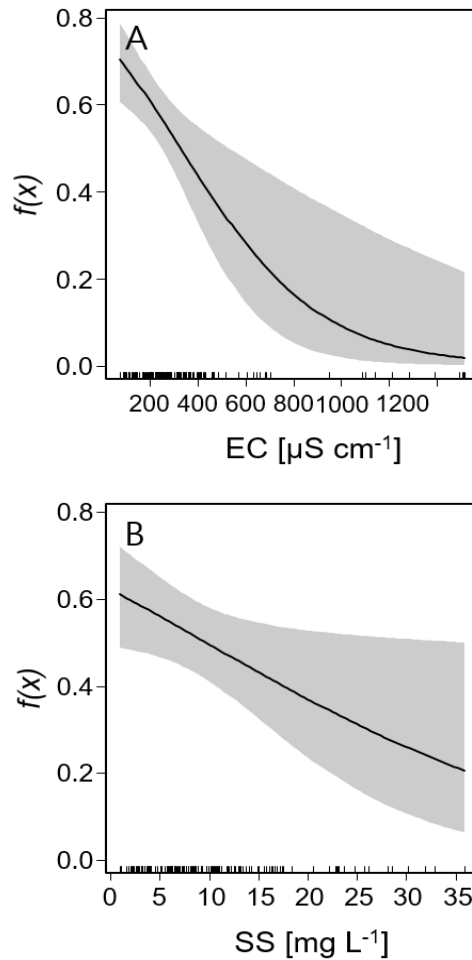


Fig. 4-2. Response curves of *Hydrilla verticillata* for environmental gradients in generalized additive models (GAMs). The vertical axes represent the probabilities of occurrence, and shaded bands show the 95% confidence interval. Rug plots on the x-axis show data points. EC, electrical conductivity; SS, suspended solids.

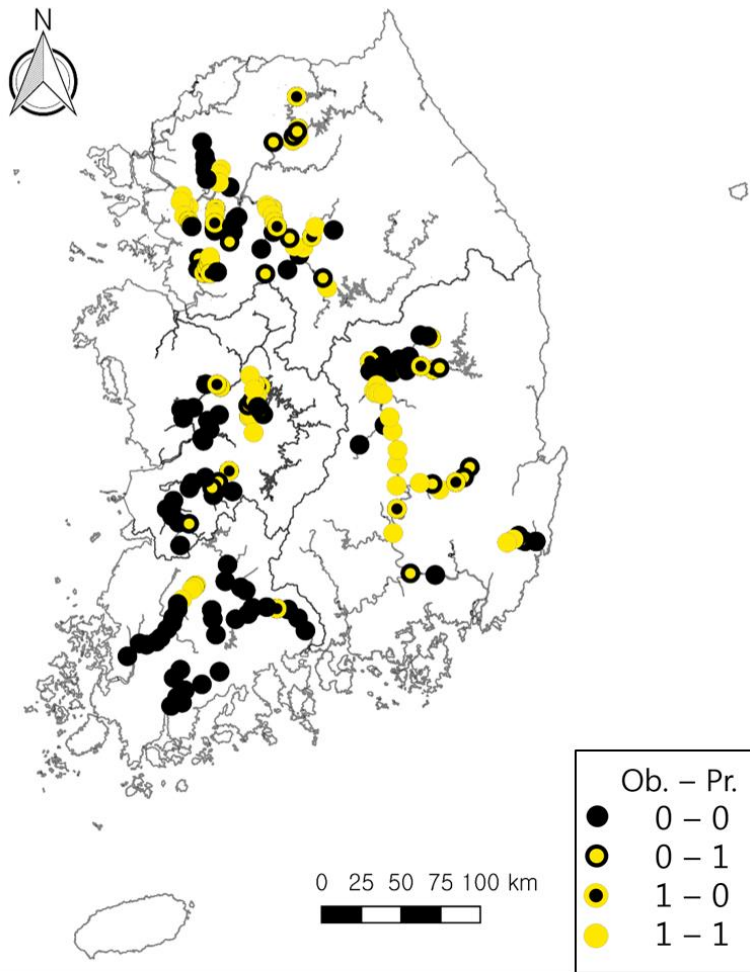


Fig. 4-3. Predicted and observed habitat suitability of *Myriophyllum spicatum* based on generalized additive models (GAMs). Observed occurrence (Ob.) is overlaid with the predicted occurrence (Pr.). The outer circle indicates the observed distribution, and the inner circle represents the predicted distribution. Yellow indicates presence (1) and black indicates absence (0). The same color for the outer and inner circles shows that observations and predictions coincide. A black outer circle with a yellow inner circle indicates a false positive, and a yellow outer with a black inner circle indicates a false negative.

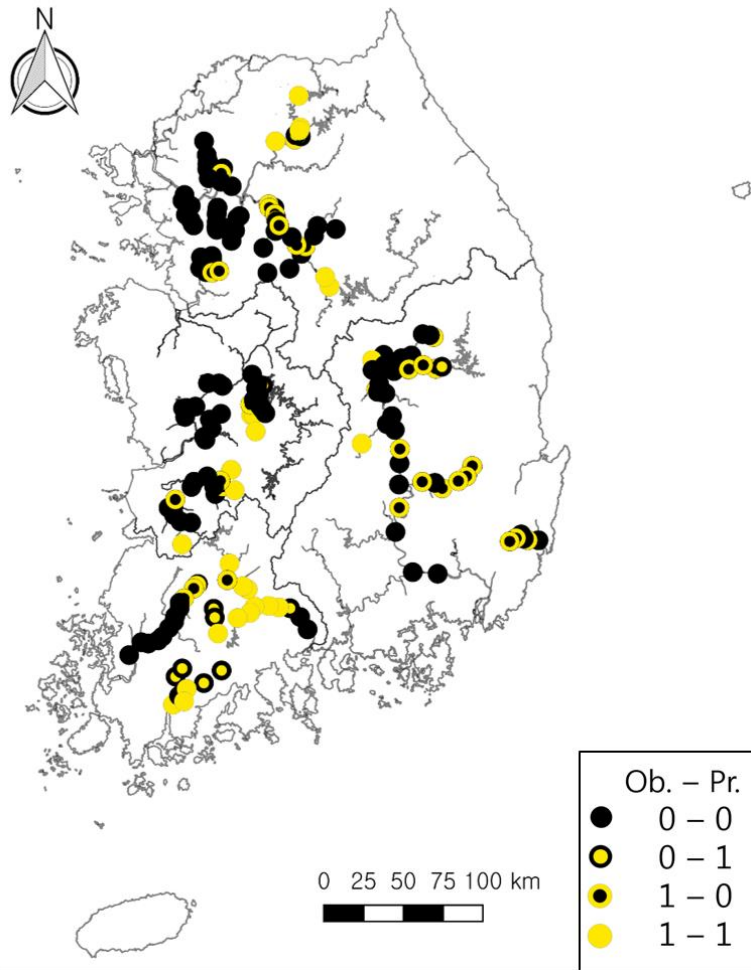


Fig. 4-4. Predicted and observed habitat suitability of *Hydrilla verticillata* based on generalized additive models (GAMs). Observed occurrence (Ob.) is overlaid with the predicted occurrence (Pr.). The outer circle indicates the observed distribution, and the inner circle represents the predicted distribution. Yellow indicates presence (1) and black indicates absence (0). The same color for the outer and inner circles shows that observations and predictions coincide. A black outer circle with a yellow inner circle indicates a false positive, and a yellow outer with a black inner circle indicates a false negative.

4.3.2. Model validation and field verification

To assess model performances for each species, I compared predicted potential habitats with observed habitats using the confusion matrix (Table 4-3). I observed accuracy rates of 0.74 for *Myriophyllum spicatum* and 0.75 for *Hydrilla verticillata*. For *M. spicatum*, AUC = 0.84 and kappa = 0.46 were observed when I applied a threshold of 0.536. For *H. verticillata*, I detected AUC = 0.79 and kappa = 0.39 when the threshold was 0.492. Based on the field verification, we observed accuracy rates of 76% for the two species (Table 4-4). The accuracy rates of 0.76 for the two species were observed. In addition, we established AUC values of 0.75 for *M. spicatum* and 0.82 for *H. verticillata*, and kappa values of 0.44 for *M. spicatum* and 0.25 for *H. verticillata*.

Table 4-3. Comparison of predicted and observed distributions of *Myriophyllum spicatum* and *Hydrilla verticillata* during model building. Predicted values were obtained from the fitted probability of presence using the Youden index to apply a threshold probability: 0.536 for *M. spicatum* and 0.492 for *H. verticillata*

Species	Contents	Predicted Absence	Predicted Presence	Total
<i>M. spicatum</i>	Observed Absence	91	23	114
	Observed Presence	29	54	83
	Total	120	77	197
	Correct prediction	$(91+54)/197 = 0.74$		
	Error of commission	$23/114 = 0.20$		
	Error of omission	$29/83 = 0.35$		
	AUC	0.84		
	Kappa	0.46		
<i>H. verticillata</i>	Observed Absence	115	13	128
	Observed Presence	37	32	69
	Total	152	45	197
	Correct prediction	$(115+32)/197 = 0.75$		
	Error of commission	$13/128 = 0.10$		
	Error of omission	$37/69 = 0.54$		
	AUC	0.79		
	Kappa	0.39		

Table 4-4. Comparison of predicted and observed distributions of *Myriophyllum spicatum* and *Hydrilla verticillata* at the model confirmation stage. Predicted values were obtained from the fitted probability of presence using the Youden index to apply a threshold probability: 0.536 for *M. spicatum* and 0.492 for *H. verticillata*

Species	Contents	Predicted Absence	Predicted Presence	Total
<i>M. spicatum</i>	Observed Absence	23	6	29
	Observed Presence	4	8	12
	Total	27	14	41
	Correct prediction	$(23+8)/41 = 0.76$		
	Error of commission	$6/29 = 0.21$		
	Error of omission	$4/12 = 0.33$		
	AUC	0.75		
	Kappa	0.44		
<i>H. verticillata</i>	Observed Absence	28	2	30
	Observed Presence	8	3	11
	Total	36	5	41
	Correct prediction	$(28+3)/41 = 0.76$		
	Error of commission	$2/30 = 0.07$		
	Error of omission	$8/11 = 0.73$		
	AUC	0.82		
	Kappa	0.25		

4.4. Discussion

In this study, we identified water environmental factors that characterize the potential habitats of *Myriophyllum spicatum* and *Hydrilla verticillata* using GAMs, namely, chlorophyll *a*, electrical conductivity, nitrate nitrogen, suspended solids, water temperature, water depth, and water velocity. GAMs are very useful for describing the complex relationships between response variables and environmental factors (Cheng and Gallinat 2004); however, these models explained low proportions of deviance (Table 4-2). This can be explained by the patchy distribution of submerged macrophytes, which cannot be fully explained by the selected variables (Lehmann 1998). Nevertheless, based on the model evaluation procedures, the response curves for each variable enabled us to infer general trends and we could adapt models to other locations around the world. Few studies have used GAMs to evaluate the habitat suitability of *M. spicatum* and *H. verticillata*, which are invasive in many countries.

4.4.1. GAM results and environmental factors

The abundance and distribution of submerged macrophytes in river ecosystems are related to water quality conditions (Nieder et al. 2004), water depth, and water velocity (Sousa 2011). I found that variables associated with water environmental factors were important determinants of the distributions of *Myriophyllum spicatum* and *Hydrilla verticillata*, especially chlorophyll *a*, electrical conductivity, nitrate nitrogen, suspended solids, water temperature, water depth, and water velocity. Gradients of these variables also determine potential habitats for submerged

macrophytes in previous studies (Dodkins et al. 2005, Lacoul and Freedman 2006, Franklin et al. 2008).

A higher temperature within optimal ranges usually promotes a higher chlorophyll *a* concentration and productivity as well as a greater abundance of submerged macrophytes (Barko et al. 1986). However, competition for light between aquatic plants and phytoplankton may limit plant growth and even result in the disappearance of taxa (Rybicki and Landwehr 2007, Bornette and Puijalon 2011). These results demonstrated that the occurrence of submerged macrophytes increased for low concentrations of chlorophyll *a*, and decreased for high concentrations. Furthermore, the adaptability of submerged macrophytes to low temperatures may play a role in interspecific competition because the optimal water temperature for submerged macrophytes is 28–32°C (Barko et al. 1986).

Plant growth usually increases as the concentration of nutrients in water and sediment increases (Van et al. 1999, Yu et al. 2010, Sousa 2011). Kennedy et al. (2009) found that *Hydrilla verticillata* could thrive not only in eutrophic waters, but also in oligotrophic waters. According to Sousa (2011), however, eutrophic conditions may have negative effects on *H. verticillata* growth via the proliferation of plankton, which compete with submerged macrophytes for light and nutrients. Electrical conductivity, as a measure of the chemicals summary variable (Heegaard et al. 2001), may affect macrophyte composition and be unfavorable for submerged macrophytes that are sensitive to eutrophication (Thomaz et al. 2003, Lauridsen et al. 2015). The occurrence of *H. verticillata* was high when electrical conductivity was low in oligotrophic water (Fig. 4-2). Nitrogen is a key element for aquatic plants, which use nitrate as a nitrogen source (Bornette and Puijalon 2011). In this study, occurrence of *Myriophyllum spicatum* was high as nitrate nitrogen increases.

However, abundance and diversity of submerged macrophytes were negatively related to nitrogen concentration (Rybicki and Landwehr 2007, Orth et al. 2010).

I detected abundant *Myriophyllum spicatum* in water at depths of 0.7–1.0 m, and a decreased abundance in deeper water (Fig. 4-1). This result concurs with a previous study; Angradi et al. (2013) observed that the optimal depth for submerged macrophytes is ~1.2 m and <1 m in turbid conditions. However, an increase in water depth causes a light deficiency for submerged macrophytes (Bornette and Puijalon 2011), thereby decreasing the rate of photosynthesis. Shallow water bodies allow more light penetration, provided that the water is not turbid (Narumalani et al. 1997). Lower water clarity owing to sediments, turbidity, and nutrients can reduce the water depth and spatial distribution for growth and survival of submerged macrophytes (Dar et al. 2014, Patrick et al. 2014). Consequently, as depth increases or water clarity decreases, light availability for photosynthesis may diminish (Lacoul and Freedman 2006).

Based on the velocity response curve, I observed a decrease in *Myriophyllum spicatum* abundance for values of up to ~0.4 m/s and an increase for higher values (Fig. 4-1). In general, the biomass and richness of submerged macrophytes are high at 0.3–0.4 m/s, and lower at higher velocities (Lacoul and Freedman 2006). A number of water velocity readings were at 0 m/s, with an average of 0.1 m/s and a median of 0 m/s. Surveyed sites were close to lentic conditions; accordingly, I could not exactly evaluate the velocity response of *M. spicatum*. Submerged macrophytes are absent in high-flow habitats, indicating a failure to establish and colonize (Lacoul and Freedman 2006). Periphyton is sheltered by submerged macrophytes, resulting in light limitation for macrophytes and controlled photosynthesis in submerged macrophytes (Strand and Weisner 2001, Riis and Biggs 2003). Moderate flow can

encourage submerged macrophytes growth by continuously washing photosynthetic tissues covered with epiphytic algae (Strand and Weisner 1996, Lehmann 1998).

4.4.2. Potential habitat predictions

I did not develop GIS-based predictive maps to identify potential habitats for submerged macrophytes because it was difficult to construct a bathymetric map of all rivers and streams in South Korea. I present maps showing areas of agreement between observations and predictions. Although I did not generate spatial maps interpolated with predicted probabilities, I was able to detect areas with abundant submerged macrophytes in the four rivers.

Correct and incorrect predictions in a confusion matrix indicate the strength of predictions (Peters et al. 2007). The misclassified sites in the predicted distribution according to GAMs were related to channel structure, rather than water quality. Most of these sites were confluence points, i.e., sites at which two channels met, each carrying independent influxes and sediment discharge (Benda et al. 2004). To examine false positive errors (commission error; observation = 0 and prediction = 1), I considered the characteristics of survey sites at confluence points that connected relatively larger tributaries to main water bodies. Confluences have been described as biodiversity hot spots with physical heterogeneity and habitat complexity owing to diverse physical, chemical, and biological attributes resulting from tributary streams (Kiffney et al. 2006, Rice et al. 2006). At these sites, I expected to observe submerged macrophytes; however, their distributions were discontinuous and bed sediment size and flow properties were unstable (Rice et al. 2006). Rare high-velocity conditions and the maintenance of stable substrata are necessary for submerged macrophytes colonization (Riis and Biggs 2003). False positive results

imply that submerged macrophytes did not have an opportunity to disperse to a suitable habitat (Buchan and Padilla 2000).

I observed false negative errors (omission error; observation = 1 and prediction = 0) at study sites that were typically downstream of confluence points connecting relatively small tributaries and irrigation ditches with the potential for submerged macrophytes dispersal. *Myriophyllum spicatum* and *Hydrilla verticillata* are found in rivers, lakes, irrigation ditches, and other waterways (Netherland 1997, Eiswerth et al. 2000). Their primary dispersal strategy is vegetative reproduction by fragmentation, moving through small waterways and then establishing at channel junctions. Vegetative reproduction by stem fragmentation is an efficient mechanism for dispersal, colonization, and overwintering (Sousa 2011, Xie et al. 2013). The conditions downstream of small tributaries are sufficiently stable for submerged macrophytes inhabitation. Submerged macrophytes habitats are regulated by a variety of factors, varying within not only whole streams, but also smaller stream reaches (Riis et al. 2001).

I observed high accuracy rates for each species model (0.74 for *Myriophyllum spicatum* and 0.75 for *Hydrilla verticillata*), but low proportions of variation explained by the models. We observed kappa values (which were dependent on a threshold) of 0.46 for *M. spicatum* and 0.39 for *H. verticillata*, indicating a fair model fit. In addition, I observed AUC values (independent of threshold values) of 0.84 for *M. spicatum* and 0.79 for *H. verticillata*, indicating satisfactory predictive ability. According to the AUC and kappa values, model performance was good for both species. Field verification to validate favorable potential habitats for *M. spicatum* and *H. verticillata* confirmed model performance, supporting their good prediction abilities, based on accuracy rates, AUC, and kappa values, except for the kappa value

(0.25) of *H. verticillata*.

Although GAMs do not provide superior predictive performance compared with other models (Austin 2007), they are flexible enough to model relationships between occurrences of submerged macrophytes and environmental factors (Murase et al. 2009). Habitats for submerged macrophytes are characterized by a complex set of physical, chemical, and biological parameters. In this study, the modeling of potential habitats for submerged macrophytes was in good agreement, despite only considering water chemicals, water depth, and water velocity. However, a reasonable possibility of prediction errors is the reason why the realized niches of submerged macrophytes were not completely explained by the variables that I selected and added to GAMs. I measured water depth and water velocity once in normal conditions, and I used water chemical data that were averaged over 4 years. Even though a lack of long-term monitoring data for water depth and velocity at the study sites is a source of uncertainty, I was able to overcome uncertainties by surveying diverse environmental conditions, varying from tributaries to rivers. In addition, to improve the predictive accuracy, it is necessary to consider physical factors, such as flow regime, channel connectivity, channel slope, channel bed, shoreline conditions, and land cover type in the basin (Buchan and Padilla 2000, Patrick et al. 2014). Biological factors, including competition, herbivory, and disease, are also important habitat determinants (Lacoul and Freedman 2006). No habitat suitability model is a complete representation of reality and these models should be validated for applications using real-world data by predictive performance evaluations focusing on the reduction of omission errors (Liu et al. 2009, Gastón and García-Viñas 2013). The distribution of submerged macrophytes could not be compared before and after water regulation; however, we are able to predict the initial distribution of *M.*

spicatum and *H. verticillata* with high invasiveness after large-scale weir construction and adapt the models throughout the world.

4.4.3. Perspectives

I inferred the habitat characteristics of *Myriophyllum spicatum* and *Hydrilla verticillata* using GAMs based on field survey data at the catchment scale. I observed that water chemicals, e.g., chlorophyll *a*, suspended solids, and nitrate nitrogen, water temperature, and electrical conductivity are important factors determining the occurrences of submerged macrophytes. This research has practical implications for the prevention or delay of the aggressive spread of *M. spicatum* and *H. verticillata* by providing a basis for river management strategies, such as information about water chemicals to improve water quality in priority areas (Barko et al. 1986). These results are also helpful to sustain aquatic ecosystem functions and biodiversity in regulated hydrological conditions by identifying priority areas for monitoring and management.

Chapter 5. General conclusion

The distribution and abundance of submerged macrophytes have been observed along four major rivers in Korea. The loss of lotic habitats has resulted in the loss of plants and animals with lifeform characteristics that are restricted to flowing water (Dynesius and Nilsson 1994). Because submerged macrophytes can act as both a storage reservoir for particulate materials during the growing season and as a source of particulate matter during vegetative senescence (Dawson 1980), studies in submerged macrophytes are important.

During the study period, *Hydrilla verticillata*, *Myriophyllum spicatum*, and *Potamogeton crispus* were the most abundant submerged plants in the four major rivers. The occurrence of submerged macrophytes was related to BOD and light availability, such as chlorophyll *a* concentrations, suspended solid concentrations, and water temperature during the growing season. These four environmental factors were significantly lower in sites containing submerged macrophytes than in non-vegetated sites. Nutrient concentration was not an important factor affecting occurrences of submerged macrophytes.

At two monitoring sites (Yangpyeong and Sangju sites), *Najas marina* had become established and was an important species over the three years. Species in *Vallisneria natans* community had relatively even coverage and this community exhibited the highest diversity. Ammonium nitrogen, nitrate nitrogen, and water velocity of the river water strongly influenced the Shannon diversity index and species richness, both of which decreased with high nutrient concentrations and rapid water flow. In summary, submerged macrophyte diversity was highest under low productivity and low disturbance conditions.

The distribution of *Myriophyllum spicatum* in the four major rivers was likely limited by water chemistry conditions including chlorophyll *a* and nitrate nitrogen

levels. In addition, suspended solids, water temperature, water depth, and water velocity affected the distribution of *M. spicatum*. Habitat factors affecting *Hydrilla verticillata* distribution were electrical conductivity and suspended solid levels.

Monitoring of vegetation and environmental conditions in river ecosystems is important because dispersal and composition of submerged macrophytes are affected by both water quality factors and water flow. In this study, it was difficult to predict accurately distributions of submerged macrophytes in the four rivers because chemical, physical, and geomorphological factors data are not enough. Although some geomorphological and hydrological factors were not included in this study, the results did provide information on the distribution of submerged macrophytes in the studied rivers and on potential submerged macrophytes habitats. Such information could affect the management of river ecosystems after the construction of large-scale weirs.

Submerged macrophytes, as a primary producer, provides habitats and refuges for periphyton, invertebrates, and fish; however, overabundant submerged macrophytes can slow water velocity and lower dissolved oxygen levels. Generally, dense submerged macrophytes result in eutrophication, which in turn can lead to a decrease in, or even a disappearance of, submerged macrophytes. Both the composition and distribution of submerged macrophytes are linked to water quality, other organisms and their habitat, and water resource use. Because of the various positive and negative effects of submerged macrophytes on river ecosystems, simultaneous conservation and management of submerged macrophytes to maintain river health and ecosystem diversity should be encouraged. Relatively broad methods for the control of dense populations of submerged macrophytes include the use of herbicides, herbivores (fish or waterfowl), and mechanical removal; however,

those methods can have high costs and negative effects on rivers (Kenneth 1996).

This research shows that BOD, chlorophyll *a*, suspended solid levels and water temperature are related to occurrences of submerged macrophytes. Moreover, the ammonium nitrogen, nitrate nitrogen, and velocity of river water affect submerged macrophyte diversity. Since occurrence and diversity of submerged macrophytes are limited by water quality and water velocity, a challenge facing water managers is the need to consider both water quality, especially water clarity, and habitat heterogeneity for aquatic organisms, including invertebrates, fish, and waterfowl. Restoring a river to a free-flowing condition by the removal of unnecessary weirs can improve water quality and aquatic habitats, allow organisms to migrate freely, and enhance the overall biodiversity of the river's ecosystem.

Sustainable management and conservation of river systems is becoming more important in order to reduce threats to aquatic biodiversity and the functioning of a natural river ecosystem. Consideration of both negative and positive effects of submerged macrophytes should be stressed when considering management or conservation actions. Thus, an integrated approach is needed to solve submerged macrophytes-related problems. Moreover, long-term solutions to such problems are needed. Based on the results of this study, prior to the development and implementation of management approaches, it is necessary to determine the ecological characteristics of submerged macrophytes as they relate to environmental factors and the prediction of submerged macrophytes distribution. In particular, preservation of free-flowing rivers with various hydrological features is needed to provide the water quality needed to ensure submerged macrophyte diversity and to limit submerged macrophytes abundance to an appropriate level.

There is a need for further research on precise estimation of abundance and

distribution of submerged macrophytes in order to manage appropriately river ecosystems. A possible weakness of this study is that both water velocity and water depth data from only one measurement at each sampling site were included in the analysis. To contribute a fuller description of the effects of water velocity and water depth on submerged macrophytes, future studies should include repetitive measurements and data from rainy and dry seasons. In addition, future studies should examine the river's physical and hydrological regimes, such as discharge, drainage area, and channel features because submerged macrophytes in freshwater ecosystems is influenced by a variety of factors in a complex manner. Interspecific competition among submerged macrophyte species can occur within relatively homogeneous environments where different species cohabit (McCreary 1991), thus competitive factors should also be considered in future studies. Accounting for all of these relevant chemical, physical, and biological factors could improve the model predictability of submerged macrophytes habitat.

In this study, the characteristics of river ecosystems after large-scale weir construction were examined. Previous assessments of river longitudinal connectivity based on species composition and distribution of submerged macrophytes, and environmental variables have not been undertaken in Korea. To assess the effects of river disconnectivities caused by physical barriers, research studies that use structural equation modeling should be undertaken.

The effects of warmer water temperatures resulting from climate change on submerged macrophytes communities can not be predicted easily. Warmer water condition will favor expansion and senescence of submerged macrophytes communities and will induce algal blooms. Monitoring and prediction of changes to submerged macrophytes communities are necessary under such long-term elevated

water temperature scenarios.

References

- Abukawa, K., M. Yamamuro, Z. Kikvidze, A. Asada, C. Xu, and K. Sugimoto. 2013. Assessing the biomass and distribution of submerged aquatic vegetation using multibeam echo sounding in Lake Towada, Japan. *Limnology* **14**:39-42.
- Agami, M., S. Beer, and Y. Waisel. 1986. The morphology and physiology of turions in *Najas marina* L. in Israel. *Aquatic Botany* **26**:371-376.
- Agami, M., and Y. Waisel. 2002. Competitive relationships between two water plant species: *Najas marina* L. and *Myriophyllum spicatum* L. *Hydrobiologia* **482**:197-200.
- Airolidi, L., D. Balata, and M. W. Beck. 2008. The Gray Zone: Relationships between habitat loss and marine diversity and their applications in conservation. *Journal of Experimental Marine Biology and Ecology* **366**:8-15.
- Alahuhta, J., J. Heino, and M. Luoto. 2011. Climate change and the future distributions of aquatic macrophytes across boreal catchments. *Journal of Biogeography* **38**:383-393.
- Alday, J. G., R. H. Marrs, and C. Martínez-Ruiz. 2011. Vegetation succession on reclaimed coal wastes in Spain: the influence of soil and environmental factors. *Applied Vegetation Science* **14**:84-94.
- Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* **43**:1223-1232.
- Almeida, E. F., R. B. Oliveira, R. Mugnai, J. L. Nessimian, and D. F. Baptista. 2009. Effects of small dams on the benthic community of streams in an Atlantic forest area of southeastern Brazil. *International Review of Hydrobiology* **94**:179-193.

- Andersson, E., C. Nilsson, and M. E. Johansson. 2000. Effects of river fragmentation on plant dispersal and riparian flora. *Regulated Rivers: Research & Management* **16**:83-89.
- Angeler, D. G., and S. Drakare. 2013. Tracing alpha, beta, and gamma diversity responses to environmental change in boreal lakes. *Oecologia* **172**:1191-1202.
- Angradi, T. R., M. S. Pearson, D. W. Bolgrien, B. J. Bellinger, M. A. Starry, and C. Reschke. 2013. Predicting submerged aquatic vegetation cover and occurrence in a Lake Superior estuary. *Journal of Great Lakes Research* **39**:536-546.
- Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* **16**:743-753.
- Arber, A. 1920. *Water Plants*. Cambridge University Press, Cambridge, UK.
- Arthaud, F., D. Vallod, J. Robin, A. Wezel, and G. Bornette. 2013. Short-term succession of aquatic plant species richness along ecosystem productivity and dispersal gradients in shallow lakes. *Journal of Vegetation Science* **24**:148-156.
- Austin, M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling* **200**:1-19.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**:101-118.
- Austin, M. P., and J. A. Meyers. 1996. Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. *Forest Ecology and Management* **85**:95-106.
- Baattrup-Pedersen, A., and T. Riis. 1999. Macrophyte diversity and composition in relation to substratum characteristics in regulated and unregulated Danish streams. *Freshwater Biology* **42**:375-385.

- Barko, J., M. Adams, and N. Clesceri. 1986. Environmental factors and their consideration in the management of submersed aquatic vegetation: a review. *Journal of Aquatic Plant Management* **24**:1-10.
- Barko, J. W., D. Gunnison, and S. R. Carpenter. 1991. Sediment interactions with submersed macrophyte growth and community dynamics. *Aquatic Botany* **41**:41-65.
- Barrat-Segretain, M. H. 1996. Strategies of reproduction, dispersion, and competition in river plants: a review. *Vegetatio* **123**:13-37.
- Barrett, S. C., C. G. Eckert, and B. C. Husband. 1993. Evolutionary processes in aquatic plant populations. *Aquatic Botany* **44**:105-145.
- Bastow Wilson, J. 2012. Species presence/absence sometimes represents a plant community as well as species abundances do, or better. *Journal of Vegetation Science* **23**:1013-1023.
- Beck, K. G., K. Zimmerman, J. D. Schardt, J. Stone, R. R. Lukens, S. Reichard, J. Randall, A. A. Cangelosi, D. Cooper, and J. P. Thompson. 2008. Invasive species defined in a policy context: recommendations from the Federal Invasive Species Advisory Committee. *Invasive Plant Science and Management* **1**:414-421.
- Benda, L., K. Andras, D. Miller, and P. Bigelow. 2004. Confluence effects in rivers: interactions of basin scale, network geometry, and disturbance regimes. *Water Resources Research* **40**:W05402.
- Bergfur, J., and C. Sundberg. 2014. Leaf-litter-associated fungi and bacteria along temporal and environmental gradients in boreal streams. *Aquatic Microbial Ecology* **73**:225-234.
- Bilotta, G. S., and R. E. Brazier. 2008. Understanding the influence of suspended

- solids on water quality and aquatic biota. *Water Research* **42**:2849-2861.
- Bolpagni, R., A. Laini, and M. M. Azzella. 2016. Short-term dynamics of submerged aquatic vegetation diversity and abundance in deep lakes. *Applied Vegetation Science* **19**:711-723.
- Borchers, D. L., S. T. Buckland, I. G. Priede, and S. Ahmadi. 1997. Improving the precision of the daily egg production method using generalized additive models. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:2727-2742.
- Borgnis, E., and K. E. Boyer. 2016. Salinity tolerance and competition drive distributions of native and invasive submerged aquatic vegetation in the upper San Francisco estuary. *Estuaries and Coasts* **39**:707-717.
- Bornette, G., and S. Puijalon. 2011. Response of aquatic plants to abiotic factors: a review. *Aquatic Sciences* **73**:1-14.
- Boylen, C. W., and R. B. Sheldon. 1976. Submergent macrophytes: growth under winter ice cover. *Science* **194**:841-842.
- Bučas, M., U. Bergström, A.-L. Downie, G. Sundblad, M. Gullström, M. von Numers, A. Šiaulys, and M. Lindegarth. 2013. Empirical modelling of benthic species distribution, abundance, and diversity in the Baltic Sea: evaluating the scope for predictive mapping using different modelling approaches. *ICES Journal of Marine Science: Journal du Conseil* **70**:1233-1243.
- Buchan, L. A. J., and D. K. Padilla. 2000. Predicting the likelihood of Eurasian watermilfoil presence in lakes, a macrophyte monitoring tool. *Ecological Applications* **10**:1442-1455.
- Buisson, L., L. Blanc, and G. Grenouillet. 2008. Modelling stream fish species distribution in a river network: the relative effects of temperature versus physical factors. *Ecology of Freshwater Fish* **17**:244-257.

- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* **30**:492-507.
- Burnham, K., and D. Anderson. 1998. *Model selection and inference: a practical information-theoretic approach* Springer-Verlag. New York.
- Canfield, D., K. Langeland, S. Linda, and W. Haller. 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. *Journal of Aquatic Plant Management* **23**:25-28.
- Capers, R. S., R. Selsky, and G. J. Bugbee. 2010. The relative importance of local conditions and regional processes in structuring aquatic plant communities. *Freshwater Biology* **55**:952-966.
- Caraco, N., J. Cole, S. Findlay, and C. Wigand. 2006. Vascular plants as engineers of oxygen in aquatic systems. *Bioscience* **56**:219-225.
- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**:426-429.
- Carpenter, S. R. 1980. The decline of *Myriophyllum spicatum* in a eutrophic Wisconsin lake. *Canadian Journal of Botany* **58**:527-535.
- Catford, J. A., B. J. Downes, C. J. Gippel, and P. A. Vesk. 2011. Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. *Journal of Applied Ecology* **48**:432-442.
- Chambers, P. A. 1987. Light and nutrients in the control of aquatic plant community structure. II. In situ observations. *Journal of Ecology* **75**:621-628.
- Chambers, P. A., R. E. DeWreede, E. A. Irlandi, and H. Vandermeulen. 1999. Management issues in aquatic macrophyte ecology: a Canadian perspective. *Canadian Journal of Botany* **77**:471-487.

- Chambers, P. A., and J. Kalff. 1987. Light and nutrients in the control of aquatic plant community structure. I. In situ experiments. *Journal of Ecology* **75**:611-619.
- Chambers, P. A., E. E. Prepas, H. R. Hamilton, and M. L. Bothwell. 1991. Current velocity and its effect on aquatic macrophytes in flowing waters. *Ecological Applications* **1**:249-257.
- Chappuis, E., E. Gacia, and E. Ballesteros. 2014. Environmental factors explaining the distribution and diversity of vascular aquatic macrophytes in a highly heterogeneous Mediterranean region. *Aquatic Botany* **113**:72-82.
- Cheng, Y. W., and M. P. Gallinat. 2004. Statistical analysis of the relationship among environmental variables, inter-annual variability and smolt trap efficiency of salmonids in the Tucannon River. *Fisheries Research* **70**:229-238.
- Cheruvilil, K. S., and P. A. Soranno. 2008. Relationships between lake macrophyte cover and lake and landscape features. *Aquatic Botany* **88**:219-227.
- Cho, W.-C., and D.-O. Lim. 2011. Flora of the Hwang-Yong River in Gwangju area. *Journal of the Industrial Technology* **17**:61-73. (*Korean Literature*)
- Choi, H.-K. 1985. Monograph of vascular hydrophytes in Korea. Seoul National University, Seoul. (*Korean Literature*)
- Choi, H.-K. 2000. Aquatic vascular plants. Korea Research Institute of Bioscience and Biotechnology, Daejeon. (*Korean Literature*)
- Choi, J. Y., K. S. Jeong, G. H. La, H. W. Kim, K. H. Chang, and G. J. Joo. 2011. Inter-annual variability of a zooplankton community: the importance of summer concentrated rainfall in a regulated river ecosystem. *Journal of Ecology and Environment* **34**:49-58.
- Churchill, R. T. J., M. L. Schummer, S. A. Petrie, and H. A. L. Henry. 2016. Long-

- term changes in distribution and abundance of submerged aquatic vegetation and dreissenid mussels in Long Point Bay, Lake Erie. *Journal of Great Lakes Research* **42**:1060-1069.
- Clayton, J., and T. Edwards. 2006. Aquatic plants as environmental indicators of ecological condition in New Zealand lakes. *Hydrobiologia* **570**:147-151.
- Coccia, C., B. Vanschoenwinkel, L. Brendonck, L. Boyero, and A. J. Green. 2016. Newly created ponds complement natural waterbodies for restoration of macroinvertebrate assemblages. *Freshwater Biology* **61**:1640-1654.
- Connolly, S. R., and L. M. Thibaut. 2012. A comparative analysis of alternative approaches to fitting species-abundance models. *Journal of Plant Ecology* **5**:32-45.
- Dar, N. A., A. K. Pandit, and B. A. Ganai. 2014. Factors affecting the distribution patterns of aquatic macrophytes. *Limnological Review* **14**:75-81.
- Dawson, F. H. 1980. The origin, composition and downstream transport of plant material in a small chalk stream. *Freshwater Biology* **10**:419-435.
- Dawson, F. H., P. J. Raven, and M. J. Gravelle. 1999. Distribution of the morphological groups of aquatic plants for rivers in the U.K. Pages 123-130 *in* J. Caffrey, P. R. F. Barrett, M. T. Ferreira, I. S. Moreira, K. J. Murphy, and P. M. Wade, editors. *Biology, Ecology and Management of Aquatic Plants: Proceedings of the 10th International Symposium on Aquatic Weeds*, European Weed Research Society. Springer Netherlands, Dordrecht.
- Demars, B. O. L., and D. M. Harper. 1998. The aquatic macrophytes of an English lowland river system: assessing response to nutrient enrichment. *Hydrobiologia* **384**:75-88.
- Den Hartog, C., and S. Segal. 1964. A new classification of the water-plant

- communities. *Acta Botanica Neerlandica* **13**:367-393.
- Dennison, W. C., R. J. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. W. Bergstrom, and R. A. Batiuk. 1993. Assessing water quality with submersed aquatic vegetation. *Bioscience* **43**:86-94.
- Depew, D. C., A. J. Houben, T. Ozersky, R. E. Hecky, and S. J. Guildford. 2011. Submerged aquatic vegetation in Cook's Bay, Lake Simcoe: assessment of changes in response to increased water transparency. *Journal of Great Lakes Research* **37**:72-82.
- Dierberg, F. E., J. J. Juston, T. A. DeBusk, K. Pietro, and B. Gu. 2005. Relationship between hydraulic efficiency and phosphorus removal in a submerged aquatic vegetation-dominated treatment wetland. *Ecological Engineering* **25**:9-23.
- Dodkins, I. A. N., B. Rippey, and P. Hale. 2005. An application of canonical correspondence analysis for developing ecological quality assessment metrics for river macrophytes. *Freshwater Biology* **50**:891-904.
- Dong-ru, Q., W. Zhen-bin, Y. Guo-an, L. Yi-jian, and Z. Yuan-jie. 1997. Study of the ecological restoration of aquatic macrophytes in a eutrophic shallow lake. *Chinese Journal of Oceanology and Limnology* **15**:52-60.
- Downie, A.-L., M. von Numers, and C. Boström. 2013. Influence of model selection on the predicted distribution of the seagrass *Zostera marina*. *Estuarine, Coastal and Shelf Science* **121**:8-19.
- Drexler, M., and C. H. Ainsworth. 2013. Generalized additive models used to predict species abundance in the Gulf of Mexico: an ecosystem modeling tool. *PLoS ONE* **8**:e64458.
- Duarte, C. M., and J. Kalff. 1987. Latitudinal influences on the depths of maximum colonization and maximum biomass of submerged angiosperms in lakes.

- Canadian Journal of Fisheries and Aquatic Sciences **44**:1759-1764.
- Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* **266**:753-762.
- Egertson, C. J., J. A. Kopaska, and J. A. Downing. 2004. A century of change in macrophyte abundance and composition in response to agricultural eutrophication. *Hydrobiologia* **524**:145-156.
- Eiswerth, M. E., S. G. Donaldson, and W. S. Johnson. 2000. Potential environmental impacts and economic damages of Eurasian watermilfoil (*Myriophyllum spicatum*) in western Nevada and northeastern California. *Weed Technology* **14**:511-518.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. M. Overton, A. Townsend Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**:129-151.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**:38-49.
- Florentine, S. K., J. Gardner, F. P. Graz, and S. Moloney. 2013. Plant recruitment and survival as indicators of ecological restoration success in abandoned pasture land in Nurcoun, Victoria, Australia. *Ecological Processes* **2**:1-13.
- Franklin, P., M. Dunbar, and P. Whitehead. 2008. Flow controls on lowland river macrophytes: a review. *Science of the Total Environment* **400**:369-378.

- Freeman, E. A., and G. G. Moisen. 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modelling* **217**:48-58.
- Gassmann, A., M. J. W. Cock, R. Shaw, and H. C. Evans. 2006. The potential for biological control of invasive alien aquatic weeds in Europe: a review. *Hydrobiologia* **570**:217-222.
- Gastón, A., and J. I. García-Viñas. 2013. Evaluating the predictive performance of stacked species distribution models applied to plant species selection in ecological restoration. *Ecological Modelling* **263**:103-108.
- Gee, J. H. R., B. D. Smith, K. M. Lee, and S. W. Griffiths. 1997. The ecological basis of freshwater pond management for biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems* **7**:91-104.
- Gehrke, P. C., P. Brown, C. B. Schiller, D. B. Moffatt, and A. M. Bruce. 1995. River regulation and fish communities in the Murray-Darling river system, Australia. *Regulated Rivers: Research & Management* **11**:363-375.
- Grace, J. B. 1993. The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. *Aquatic Botany* **44**:159-180.
- Greet, J., R. D. Cousens, and J. A. Webb. 2013. Flow regulation is associated with riverine soil seed bank composition within an agricultural landscape: potential implications for restoration. *Journal of Vegetation Science* **24**:157-167.
- Gregor, J., and B. Maršálek. 2004. Freshwater phytoplankton quantification by chlorophyll *a*: a comparative study of in vitro, in vivo and in situ methods. *Water Research* **38**:517-522.
- Guisan, A., T. C. Edwards Jr, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological*

Modelling **157**:89-100.

- Gurnell, A. M., J. M. O'Hare, M. T. O'Hare, M. J. Dunbar, and P. M. Scarlett. 2010. An exploration of associations between assemblages of aquatic plant morphotypes and channel geomorphological properties within British rivers. *Geomorphology* **116**:135-144.
- Handley, R. J., and A. J. Davy. 2002. Seedling root establishment may limit *Najas marina* L. to sediments of low cohesive strength. *Aquatic Botany* **73**:129-136.
- Hartleb, C. F., J. D. Madsen, and C. W. Boylen. 1993. Environmental factors affecting seed germination in *Myriophyllum spicatum* L. *Aquatic Botany* **45**:15-25.
- Heegaard, E., H. H. Birks, C. E. Gibson, S. J. Smith, and S. Wolfe-Murphy. 2001. Species–environmental relationships of aquatic macrophytes in Northern Ireland. *Aquatic Botany* **70**:175-223.
- Hestir, E. L., D. H. Schoellhamer, J. Greenberg, T. Morgan-King, and S. L. Ustin. 2016. The effect of submerged aquatic vegetation expansion on a declining turbidity trend in the Sacramento-San Joaquin River Delta. *Estuaries and Coasts* **39**:1100-1112.
- Holt, C. R., D. Pfitzer, C. Scalley, B. A. Caldwell, and D. P. Batzer. 2015. Macroinvertebrate community responses to annual flow variation from river regulation: an 11-year study. *River Research and Applications* **31**:798-807.
- Hrivnák, R., J. Kochjarová, H. Oľahel'ová, P. Paľove-Balang, M. Slezák, and P. Slezák. 2014. Environmental drivers of macrophyte species richness in artificial and natural aquatic water bodies – comparative approach from two central European regions. *Annales de Limnologie - International Journal of Limnology*. **50**:269-278.

- Hudon, C. 1997. Impact of water level fluctuations on St. Lawrence River aquatic vegetation. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:2853-2865.
- Humphries, P., P. Brown, J. Douglas, A. Pickworth, R. Strongman, K. Hall, and L. Serafini. 2008. Flow-related patterns in abundance and composition of the fish fauna of a degraded Australian lowland river. *Freshwater Biology* **53**:789-813.
- Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist* **113**:81-101.
- Hwang, S.-A., S.-J. Hwang, S.-R. Park, and S.-W. Lee. 2016. Examining the relationships between watershed urban land use and stream water quality using linear and generalized additive models. *Water* **8**:155.
- Järvelä, J. 2005. Effect of submerged flexible vegetation on flow structure and resistance. *Journal of Hydrology* **307**:233-241.
- Janauer, G. A., U. Schmidt-Mumm, and B. Schmidt. 2010. Aquatic macrophytes and water current velocity in the Danube River. *Ecological Engineering* **36**:1138-1145.
- Jansson, R., C. Nilsson, and B. Renofalt. 2000. Fragmentation of riparian floras in rivers with multiple dams. *Ecology* **81**:899-903.
- Jian, Y., B. Li, J. Wang, and J. Chen. 2003. Control of turion germination in *Potamogeton crispus*. *Aquatic Botany* **75**:59-69.
- Jiménez-Valverde, A., and J. M. Lobo. 2007. Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica* **31**:361-369.
- Johansson, M. E., C. Nilsson, and E. Nilsson. 1996. Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science* **7**:593-598.
- Johnson, S. E., E. L. Mudrak, and D. M. Waller. 2014. Local increases in diversity

- accompany community homogenization in floodplain forest understories. *Journal of Vegetation Science* **25**:885-896.
- Jones, J. I., A. L. Collins, P. S. Naden, and D. A. Sear. 2012. The relationship between fine sediment and macrophytes in rivers. *River Research and Applications* **28**:1006-1018.
- Jun, K. S., and J. S. Kim. 2011. The four major rivers restoration project: impacts on river flows. *KSCE Journal of Civil Engineering* **15**:217-224.
- Körner, S. 2002. Loss of submerged macrophytes in shallow lakes in North-Eastern Germany. *International Review of Hydrobiology* **87**:375-384.
- Kautsky, L. 1988. Life strategies of aquatic soft bottom macrophytes. *Oikos* **53**:126-135.
- Kelly, M. G., N. Thyssen, and B. Moeslund. 1983. Light and the annual variation of oxygen- and carbon-based measurements of productivity in a macrophyte-dominated river. *Limnology and Oceanography* **28**:503-515.
- Kemp, W. P., S. J. Harvey, and K. M. O'Neill. 1990. Patterns of vegetation and grasshopper community composition. *Oecologia* **83**:299-308.
- Kennedy, T. L., L. A. Horth, and D. E. Carr. 2009. The effects of nitrate loading on the invasive macrophyte *Hydrilla verticillata* and two common, native macrophytes in Florida. *Aquatic Botany* **91**:253-256.
- Kenneth, A. L. 1996. *Hydrilla verticillata* (L.F.) Royle (Hydrocharitaceae), "The Perfect Aquatic Weed". *Castanea* **61**:293-304.
- Keskinkan, O., M. Z. L. Goksu, M. Basibuyuk, and C. F. Forster. 2004. Heavy metal adsorption properties of a submerged aquatic plant (*Ceratophyllum demersum*). *Bioresource Technology* **92**:197-200.
- Kiffney, P. M., C. M. Greene, J. Hall, and J. Davies. 2006. Tributary streams create

- spatial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. *Canadian Journal of Fisheries and Aquatic Sciences* **63**:2518-2530.
- Kim, D.-K., K.-S. Jeong, P. A. Whigham, and G.-J. Joo. 2007. Winter diatom blooms in a regulated river in South Korea: explanations based on evolutionary computation. *Freshwater Biology* **52**:2021-2041.
- Kim, H. J., H. C. Shin, and H. K. Choi. 2002. Taxonomy of the genus *Potamogeton* (Potamogetonaceae) in Korea. *Korean Journal of Plant Taxonomy* **32**:209-232. (*Korean Literature*)
- Kim, H. Y., M. H. Kim, H. K. Choi, D. Y. Lyang, E.-J. Shin, K. S. Lee, and H. Yi. 2010. Changes of vegetation structure according to the hydro-seral stages in the east coastal lagoons, Korea. *Journal of Wetlands Research* **12**:129-144. (*Korean Literature*)
- Kim, K., S.-N. Jin, H. Cho, and K.-H. Cho. 2012. Distribution, vegetation structure and biomass of submerged macrophytes in a small agricultural reservoir, Keumpoong Reservoir, Korea. *Korean Journal of Limnology* **45**:52-61. (*Korean Literature*)
- Kim, S.-H., J.-W. An, I.-T. Kim, U.-H. Cho, H.-J. Lee, and D.-J. Hwang. 2011. A study on the flora and distribution of vegetation in Reservoir Jangchuck. *Journal of Wetlands Research* **13**:657-664. (*Korean Literature*)
- Koch, E. W. 2001. Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* **24**:1-17.
- Kronvang, B., A. Laubel, S. E. Larsen, and N. Friberg. 2003. Pesticides and heavy metals in Danish streambed sediment. Pages 93-101 in B. Kronvang, editor. *The*

- Interactions between Sediments and Water: Proceedings of the 9th International Symposium on the Interactions between Sediments and Water, held 5–10 May 2002 in Banff, Alberta, Canada. Springer Netherlands, Dordrecht.
- Kuhn, M., and K. Johnson. 2013. Applied predictive modeling. Springer.
- Kwon, K.-Y. 2011. Growth response and change in water quality as affected by environmental condition on submerged plant. Gyeongsang National University, Jinju. (*Korean Literature*)
- Lacoul, P., and B. Freedman. 2006. Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews* **14**:89-136.
- Lah, T., Y. Park, and Y. J. Cho. 2015. The four major rivers restoration project of South Korea: an assessment of its process, program, and political dimensions. *The Journal of Environment & Development* **24**:375-394.
- Landis, J. R., and G. G. Koch. 1977. The measurement of observer agreement for categorical data. *Biometrics*:159-174.
- Lathrop, R. G., R. M. Styles, S. P. Seitzinger, and J. A. Bognar. 2001. Use of GIS mapping and modeling approaches to examine the spatial distribution of seagrasses in Barnegat Bay, New Jersey. *Estuaries* **24**:904-916.
- Lauridsen, T. L., E. Jeppesen, S. A. J. Declerck, L. De Meester, J. M. Conde-Porcuna, W. Rommens, and S. Brucet. 2015. The importance of environmental variables for submerged macrophyte community assemblage and coverage in shallow lakes: differences between northern and southern Europe. *Hydrobiologia* **744**:49-61.
- Lee, G.-j., and K. Sung. 2013. Effects of floating and submerged plants on important water environments of wetland. *Journal of Wetlands Research* **15**:289-300. (*Korean Literature*)

- Lee, T. B. 2003. Coloured flora of Korea. Hyang Mun Sa, Seoul. (*Korean Literature*)
- Lee, Y.-H. 2009. Riparian vegetation of the Taehwagang and its tributary streams (Ulsan, South Korea). Dong-A University, Busan. (*Korean Literature*)
- Lehmann, A. 1998. GIS modeling of submerged macrophyte distribution using generalized additive models. *Plant Ecology* **139**:113-124.
- Lehmann, A., E. Castella, and J. B. Lachavanne. 1997. Morphological traits and spatial heterogeneity of aquatic plants along sediment and depth gradients, Lake Geneva, Switzerland. *Aquatic Botany* **55**:281-299.
- Lehmann, A., and J.-B. Lachavanne. 1999. Changes in the water quality of Lake Geneva indicated by submerged macrophytes. *Freshwater Biology* **42**:457-466.
- Li, X., and Y. Wang. 2013. Applying various algorithms for species distribution modelling. *Integrative Zoology* **8**:124-135.
- Lim, J.-c., K.-w. An, C.-w. Lee, J.-h. Lee, and B.-k. Choi. 2016. Distribution patterns of hydrophytes by water depth distribution in Mokpo of Upo Wetland. *Journal of Ecology and Environment* **30**:308-319. (*Korean Literature*)
- Lim, Y. 2010. Distribution characteristics of hydrophytes in Korea. Soonchunhyang University, Asan. (*Korean Literature*)
- Lim, Y. S., S. M. Ma, S. T. Na, H. K. Choi, and H. C. Shin. 2005. Flora and ecological characteristics of hydrophytes in the littoral zone of Paldang Reservoir. *Korean Journal of Limnology* **38**:30-44. (*Korean Literature*)
- Lirman, D., G. Deangelo, J. Serafy, A. Hazra, D. Smith Hazra, J. Herlan, J. Luo, S. Bellmund, J. Wang, and R. Clausen. 2007. Seasonal changes in the abundance and distribution of submerged aquatic vegetation in a highly managed coastal lagoon. *Hydrobiologia* **596**:105.
- Liu, C., M. White, and G. Newell. 2009. Measuring the accuracy of species

- distribution models: a review. Pages 4241-4247 in Proceedings 18th World IMACs/MODSIM Congress. Cairns, Australia. Citeseer.
- Liu, Y., Y. Wang, and H. Huang. 2006. High interpopulation genetic differentiation and unidirectional linear migration patterns in *Myricaria laxiflora* (Tamaricaceae), an endemic riparian plant in the Three Gorges Valley of the Yangtze River. *American Journal of Botany* **93**:206-215.
- Lopatin, J., K. Dolos, H. Hernández, M. Galleguillos, and F. Fassnacht. 2016. Comparing generalized linear models and random forest to model vascular plant species richness using LiDAR data in a natural forest in central Chile. *Remote Sensing of Environment* **173**:200-210.
- Mackay, S. J., A. H. Arthington, M. J. Kennard, and B. J. Pusey. 2003. Spatial variation in the distribution and abundance of submersed macrophytes in an Australian subtropical river. *Aquatic Botany* **77**:169-186.
- Maddock, I. 1999. The importance of physical habitat assessment for evaluating river health. *Freshwater Biology* **41**:373-391.
- Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch, and D. F. Westlake. 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* **444**:71-84.
- Makkay, K., F. R. Pick, and L. Gillespie. 2008. Predicting diversity versus community composition of aquatic plants at the river scale. *Aquatic Botany* **88**:338-346.
- Manolaki, P., and E. Papastergiadou. 2016. Environmental factors influencing macrophytes assemblages in a middle-sized Mediterranean Stream. *River Research and Applications* **32**:639-651.
- McClanahan, T. R. 1986. The effect of a seed source on primary succession in a

- forest ecosystem. *Vegetatio* **65**:175-178.
- McCreary, N. J. 1991. Competition as a mechanism of submersed macrophyte community structure. *Aquatic Botany* **41**:177-193.
- McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* **14**:450-453.
- Michael Kemp, W., R. Batleson, P. Bergstrom, V. Carter, C. L. Gallegos, W. Hunley, L. Karrh, E. W. Koch, J. M. Landwehr, K. A. Moore, L. Murray, M. Naylor, N. B. Rybicki, J. Court Stevenson, and D. J. Wilcox. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: water quality, light regime, and physical-chemical factors. *Estuaries* **27**:363-377.
- Moore, K. A. 2009. Submerged aquatic vegetation of the York River. *Journal of Coastal Research*:50-58.
- Moyle, P. B., and J. F. Mount. 2007. Homogenous rivers, homogenous faunas. *Proceedings of the National Academy of Sciences* **104**:5711-5712.
- Mueller, M., J. Pander, and J. Geist. 2011. The effects of weirs on structural stream habitat and biological communities. *Journal of Applied Ecology* **48**:1450-1461.
- Murase, H., H. Nagashima, S. Yonezaki, R. Matsukura, and T. Kitakado. 2009. Application of a generalized additive model (GAM) to reveal relationships between environmental factors and distributions of pelagic fish and krill: a case study in Sendai Bay, Japan. *ICES Journal of Marine Science: Journal du Conseil* **66**:1417-1424.
- Na, H. R. 2010. Sexual system and systematics of Hydrilloideae (Hydrocharitaceae). Ajou University, Suwon. (*Korean Literature*)
- Narumalani, S., J. R. Jensen, S. Burkhalter, J. D. Althausen, and H. E. Mackey Jr.

1997. Aquatic macrophyte modeling using GIS and logistic multiple regression. *Photogrammetric Engineering and Remote Sensing* **63**:41-49.
- Nepf, H., M. Ghisalberti, B. White, and E. Murphy. 2007. Retention time and dispersion associated with submerged aquatic canopies. *Water Resources Research* **43**:W04422.
- Netherland, M. D. 1997. Turion ecology of hydrilla. *Journal of Aquatic Plant Management* **35**:1-10.
- Nieder, W. C., E. Barnaba, S. E. G. Findlay, S. Hoskins, N. Holochuck, and E. A. Blair. 2004. Distribution and abundance of submerged aquatic vegetation and *Trapa natans* in the Hudson River Estuary. *Journal of Coastal Research*:150-161.
- Nilsson, C. 1987. Distribution of stream-edge vegetation along a gradient of current velocity. *Journal of Ecology* **75**:513-522.
- Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* **308**:405-408.
- Nilsson, C., and M. Svedmark. 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Environmental Management* **30**:468-480.
- Normile, D. 2010. Restoration or devastation? *Science* **327**:1568-1570.
- O'Hare, J. M., M. T. O'Hare, A. M. Gurnell, M. J. Dunbar, P. M. Scarlett, and C. Laizé. 2011. Physical constraints on the distribution of macrophytes linked with flow and sediment dynamics in British rivers. *River Research and Applications* **27**:671-683.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. Package 'vegan'.

Community ecology package, version 2.

- Olivera-Gomez, L. D., and E. Mellink. 2013. Aquatic macrophytes within a mesohaline bay, sanctuary for Manatees (*Trichechus manatus*), on the Caribbean Coast of Mexico. *Southwestern Naturalist* **58**:216-222.
- Orth, R. J., M. R. Williams, S. R. Marion, D. J. Wilcox, T. J. Carruthers, K. A. Moore, W. M. Kemp, W. C. Dennison, N. Rybicki, and P. Bergstrom. 2010. Long-term trends in submersed aquatic vegetation (SAV) in Chesapeake Bay, USA, related to water quality. *Estuaries and Coasts* **33**:1144-1163.
- Park, S. G. 2016. Long-Term Changes of the Littoral Vegetation in the Reservoir Paldang, Korea. Inha University, Incheon. (*Korean Literature*)
- Patrick, C. J., D. E. Weller, X. Li, and M. Ryder. 2014. Effects of shoreline alteration and other stressors on submerged aquatic vegetation in subestuaries of Chesapeake Bay and the Mid-Atlantic Coastal Bays. *Estuaries and Coasts* **37**:1516-1531.
- Patrick, C. J., D. E. Weller, and M. Ryder. 2016. The relationship between shoreline armoring and adjacent submerged aquatic vegetation in Chesapeake Bay and Nearby Atlantic Coastal Bays. *Estuaries and Coasts* **39**:158-170.
- Paudel, S., and O. R. Vetaas. 2014. Effects of topography and land use on woody plant species composition and beta diversity in an arid Trans-Himalayan landscape, Nepal. *Journal of Mountain Science* **11**:1112-1122.
- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* **133**:225-245.
- Pearsall, W. H. 1918. On the classification of aquatic plant communities. *Journal of Ecology* **6**:75-84.
- Pedro, F., L. Maltchik, and I. Bianchini Jr. 2006. Hydrologic cycle and dynamics of

- aquatic macrophytes in two intermittent rivers of the semi-arid region of Brazil. *Brazilian Journal of Biology* **66**:575-585.
- Peters, J., B. D. Baets, N. E. C. Verhoest, R. Samson, S. Degroeve, P. D. Becker, and W. Huybrechts. 2007. Random forests as a tool for ecohydrological distribution modelling. *Ecological Modelling* **207**:304-318.
- Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences* **104**:5732-5737.
- Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in riparian wetlands—a test of biodiversity theory. *Ecology* **79**:94-105.
- Puijalon, S., G. Bornette, and P. Sagnes. 2005. Adaptations to increasing hydraulic stress: morphology, hydrodynamics and fitness of two higher aquatic plant species. *Journal of Experimental Botany* **56**:777-786.
- QGIS Development Team. 2016. QGIS Geographic Information System. Open Source Geospatial Foundation Project.
- Qiu, D., Z. Wu, B. Liu, J. Deng, G. Fu, and F. He. 2001. The restoration of aquatic macrophytes for improving water quality in a hypertrophic shallow lake in Hubei Province, China. *Ecological Engineering* **18**:147-156.
- R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.
- Rørslett, B. 1991. Physiological ecology of aquatic macrophytes principal determinants of aquatic macrophyte richness in northern European lakes. *Aquatic Botany* **39**:173-193.
- Ranieri, M. C., P. Gantes, and F. Momo. 2015. Diversity patterns of Pampean stream

- vegetation at different spatial scales. *Aquatic Botany* **126**:1-6.
- Rice, S. P., R. I. Ferguson, and T. B. Hoey. 2006. Tributary control of physical heterogeneity and biological diversity at river confluences. *Canadian Journal of Fisheries and Aquatic Sciences* **63**:2553-2566.
- Riis, T., and B. J. F. Biggs. 2003. Hydrologic and hydraulic control of macrophyte establishment and performance in streams. *Limnology and Oceanography* **48**:1488-1497.
- Riis, T., and I. Hawes. 2002. Relationships between water level fluctuations and vegetation diversity in shallow water of New Zealand lakes. *Aquatic Botany* **74**:133-148.
- Riis, T., K. Sand-Jensen, and S. E. Larsen. 2001. Plant distribution and abundance in relation to physical conditions and location within Danish stream systems. *Hydrobiologia* **448**:217-228.
- Riis, T., K. Sand-Jensen, and O. Vestergaard. 2000. Plant communities in lowland Danish streams: species composition and environmental factors. *Aquatic Botany* **66**:255-272.
- Riis, T., and K. A. J. Sand-Jensen. 2006. Dispersal of plant fragments in small streams. *Freshwater Biology* **51**:274-286.
- Rim, H. 2010. Soil seed bank variation along a water depth gradient in Lake Paldang. Master's thesis of Seoul National University, Seoul.
- Rolon, A. S., and L. Maltchik. 2006. Environmental factors as predictors of aquatic macrophyte richness and composition in wetlands of southern Brazil. *Hydrobiologia* **556**:221-231.
- Rooney, N., and J. Kalff. 2000. Inter-annual variation in submerged macrophyte community biomass and distribution: the influence of temperature and lake

- morphometry. *Aquatic Botany* **68**:321-335.
- Rooney, R. C., C. Carli, and S. E. Bayley. 2013. River connectivity affects submerged and floating aquatic vegetation in floodplain wetlands. *Wetlands* **33**:1165-1177.
- Ross, L. C., S. J. Woodin, A. J. Hester, D. B. A. Thompson, and H. J. B. Birks. 2012. Biotic homogenization of upland vegetation: patterns and drivers at multiple spatial scales over five decades. *Journal of Vegetation Science* **23**:755-770.
- Ryan, P. A. 1991. Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research* **25**:207-221.
- Rybicki, N. B., and V. Carter. 2002. Light and temperature effects on the growth of wild celery and *Hydrilla*. *Journal of Aquatic Plant Management* **40**:92-99.
- Rybicki, N. B., and J. M. Landwehr. 2007. Long-term changes in abundance and diversity of macrophyte and waterfowl populations in an estuary with exotic macrophytes and improving water quality. *Limnology and Oceanography* **52**:1195-1207.
- Søndergaard, M., L. S. Johansson, T. L. Lauridsen, T. B. Jørgensen, L. Liboriussen, and E. Jeppesen. 2010. Submerged macrophytes as indicators of the ecological quality of lakes. *Freshwater Biology* **55**:893-908.
- Sanchez, P., M. Demestre, L. Recasens, F. Maynou, and P. Martin. 2008. Combining GIS and GAMs to identify potential habitats of squid *Loligo vulgaris* in the Northwestern Mediterranean. *Hydrobiologia* **612**:91-98.
- Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquatic Botany* **3**:55-63.
- Sand-Jensen, K., and J. Borum. 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany*

41:137-175.

- Sand-Jensen, K. A. J., and T. O. M. Vindbæk Madsen. 1992. Patch dynamics of the stream macrophyte, *Callitriche cophocarpa*. *Freshwater Biology* **27**:277-282.
- Santamaría, L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecologica* **23**:137-154.
- Santamaría, L., and W. van Vierssen. 1997. Photosynthetic temperature responses of fresh- and brackish-water macrophytes: a review. *Aquatic Botany* **58**:135-150.
- Schlising, R. A., and E. L. Sanders. 1982. Quantitative analysis of vegetation at the Richvale Vernal Pools, California. *American Journal of Botany* **69**:734-742.
- Schook, D. M., E. A. Carlson, J. S. Sholtes, and D. J. Cooper. 2016. Effects of moderate and extreme flow regulation on *Populus* growth along the green and Yampa Rivers, Colorado and Utah. *River Research and Applications* **32**:1698-1708.
- Sculthorpe, C. D. 1985. *The biology of aquatic vascular plants* / C. D. Sculthorpe. Königstein : Koeltz Scientific Books, 1985., Königstein.
- Seddon, B. 1972. Aquatic macrophytes as limnological indicators. *Freshwater Biology* **2**:107-130.
- Segurado, P., and M. B. Araujo. 2004. An evaluation of methods for modelling species distributions. *Journal of Biogeography* **31**:1555-1568.
- Shmueli, G. 2010. To explain or to predict? *Statistical science*:289-310.
- Sing, T., O. Sander, N. Beerenwinkel, and T. Lengauer. 2005. ROCR: visualizing classifier performance in R. *Bioinformatics* **21**:3940-3941.
- Solanki, H. U., D. Bhatpuria, and P. Chauhan. 2016. Applications of generalized additive model (GAM) to satellite-derived variables and fishery data for

- prediction of fishery resources distributions in the Arabian Sea. *Geocarto International*:1-13.
- Sousa, W. 2011. *Hydrilla verticillata* (Hydrocharitaceae), a recent invader threatening Brazil's freshwater environments: a review of the extent of the problem. *Hydrobiologia* **669**:1-20.
- St-Cyr, L., P. G. C. Campbell, and K. Guertin. 1994. Evaluation of the role of submerged plant beds in the metal budget of a fluvial lake. *Hydrobiologia* **291**:141-156.
- Strand, J. A., and S. E. B. Weisner. 1996. Wave exposure related growth of epiphyton: implications for the distribution of submerged macrophytes in eutrophic lakes. *Hydrobiologia* **325**:113-119.
- Strand, J. A., and S. E. B. Weisner. 2001. Morphological plastic responses to water depth and wave exposure in an aquatic plant (*Myriophyllum spicatum*). *Journal of Ecology* **89**:166-175.
- Sultana, M., T. Asaeda, M. Ekram Azim, and T. Fujino. 2010. Morphological responses of a submerged macrophyte to epiphyton. *Aquatic Ecology* **44**:73-81.
- Swets, J. 1988. Measuring the accuracy of diagnostic systems. *Science* **240**:1285-1293.
- Takamura, N., Y. Kadono, M. Fukushima, M. Nakagawa, and B.-H. O. Kim. 2003. Effects of aquatic macrophytes on water quality and phytoplankton communities in shallow lakes. *Ecological Research* **18**:381-395.
- Tereraí, F., M. Gaertner, S. M. Jacobs, and D. M. Richardson. 2013. Eucalyptus invasions in riparian forests: effects on native vegetation community diversity, stand structure and composition. *Forest Ecology and Management* **297**:84-93.
- Thomaz, S. M., D. C. Souza, and L. M. Bini. 2003. Species richness and beta

- diversity of aquatic macrophytes in a large subtropical reservoir (Itaipu Reservoir, Brazil): the influence of limnology and morphometry. *Hydrobiologia* **505**:119-128.
- Thuiller, W., D. M. Richardson, P. Pyšek, G. F. Midgley, G. O. Hughes, and M. Rouget. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* **11**:2234-2250.
- Tian, K., G. Liu, D. Xiao, J. Sun, M. Lu, Y. Huang, and P. Lin. 2015. Ecological effects of dam impoundment on closed and half-closed wetlands in China. *Wetlands* **35**:889-898.
- Toivonen, H., and P. Huttunen. 1995. Aquatic macrophytes and ecological gradients in 57 small lakes in southern Finland. *Aquatic Botany* **51**:197-221.
- Turner, W., S. Spector, N. Gardiner, M. Fladeland, E. Sterling, and M. Steininger. 2003. Remote sensing for biodiversity science and conservation. *Trends in Ecology & Evolution* **18**:306-314.
- Van, T. K., G. S. Wheeler, and T. D. Center. 1999. Competition between *Hydrilla verticillata* and *Vallisneria americana* as influenced by soil fertility. *Aquatic Botany* **62**:225-233.
- VanDerWal, J., L. Falconi, S. Januchowski, L. Shoo, and C. Storlie. 2014. SDMTools: species distribution modelling tools: tools for processing data associated with species distribution modelling exercises. R package version:1.1-221.
- Vestergaard, O., and K. Sand-Jensen. 2000. Aquatic macrophyte richness in Danish lakes in relation to alkalinity, transparency, and lake area. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:2022-2031.
- Wedding, L., and M. M. Yoklavich. 2015. Habitat-based predictive mapping of rockfish density and biomass off the central California coast. *Marine Ecology*

- Progress Series **540**:235-250.
- Welsh, R. P. H., and P. Denny. 1980. The uptake of lead and copper by submerged aquatic macrophytes in two English lakes. *Journal of Ecology* **68**:443-455.
- Whitehead, P. G., R. L. Wilby, R. W. Battarbee, M. Kernan, and A. J. Wade. 2009. A review of the potential impacts of climate change on surface water quality. *Hydrological Sciences Journal* **54**:101-123.
- Wickham, H. 2009. *ggplot2: Elegant graphics for data analysis*. New York, NY : Springer-Verlag New York, 2009., New York, NY.
- Wilson, C. O., and Q. Weng. 2011. Simulating the impacts of future land use and climate changes on surface water quality in the Des Plaines River watershed, Chicago Metropolitan Statistical Area, Illinois. *Science of the Total Environment* **409**:4387-4405.
- Woo, H. 2010. Trends in ecological river engineering in Korea. *Journal of Hydro-environment Research* **4**:269-278.
- Wood, S. N. 2000. Modelling and smoothing parameter estimation with multiple quadratic penalties. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **62**:413-428.
- Xie, D., D. Yu, W. H. You, and L. G. Wang. 2013. Morphological and physiological responses to sediment nutrients in the submerged macrophyte *Myriophyllum spicatum*. *Wetlands* **33**:1095-1102.
- Yee, T. W., and N. D. Mitchell. 1991. Generalized additive models in plant ecology. *Journal of Vegetation Science* **2**:587-602.
- Yeo, R. R. 1965. Life history of sago pondweed. *Weeds* **13**:314-321.
- Yi, Y. m., D. Kang, and K. Sung. 2009. Germination experiments using natural wetland soil for introducing non-emergent plants into a constructed wetland.

- Journal of Wetlands Research **11**:39-48. (*Korean Literature*)
- You, J.-H., S.-G. Jung, K.-H. Pakr, K.-T. Kim, and W.-S. Lee. 2008. Flora in Ahnshim wetland, Daegu metropolitan city. Korean Journal of Plant Resources **21**:162-170. (*Korean Literature*)
- Yu, H., C. Ye, X. Song, and J. Liu. 2010. Comparative analysis of growth and physio-biochemical responses of *Hydrilla verticillata* to different sediments in freshwater microcosms. Ecological Engineering **36**:1285-1289.
- Zhang, C., X. Gao, L. Wang, and X. Chen. 2015. Modelling the role of epiphyton and water level for submerged macrophyte development with a modified submerged aquatic vegetation model in a shallow reservoir in China. Ecological Engineering **81**:123-132.
- Zhang, Y., X. Liu, B. Qin, K. Shi, J. Deng, and Y. Zhou. 2016. Aquatic vegetation in response to increased eutrophication and degraded light climate in eastern lake Taihu: implications for lake ecological restoration. Scientific Reports **6**:23867.
- Zhao, J., J. Cao, S. Tian, Y. Chen, S. Zhang, Z. Wang, and X. Zhou. 2014. A comparison between two GAM models in quantifying relationships of environmental variables with fish richness and diversity indices. Aquatic Ecology **48**:297-312.
- Zhou, N., W. Hu, J. Deng, J. Zhu, W. Xu, and X. Liu. 2016. The effects of water depth on the growth and reproduction of *Potamogeton crispus* in an *in situ* experiment. Journal of Plant Ecology.
- Zhou, S., T. Tang, N. Wu, X. Fu, and Q. Cai. 2008. Impacts of a small dam on riverine zooplankton. International Review of Hydrobiology **93**:297-311.
- Zimmermann, N. E., T. C. Edwards, G. G. Moisen, T. S. Frescino, and J. A. Blackard. 2007. Remote sensing-based predictors improve distribution models of rare,

early successional and broadleaf tree species in Utah. *Journal of Applied Ecology* **44**:1057-1067.

Zou, W., L. Yuan, and L. Zhang. 2013. Analyzing the spectral response of submerged aquatic vegetation in a eutrophic lake, Shanghai, China. *Ecological Engineering* **57**:65-71.

Zuur, A. F., and G. J. Pierce. 2004. Common trends in northeast Atlantic squid time series. *Journal of Sea Research* **52**:57-72.

Appendix 1. Similarity percentage (SIMPER) analyses of submerged macrophytes representing the occurrence (occurrence rate) of major taxa between the four rivers. Taxa with the lowest contribution to dissimilarities, such as *Potamogeton octandrus*, *P. oxyphyllus*, and *Najas graminea* are not shown

	Geum River-Han River		Geum River-Nakdong River		Geum River-Yeongsan River	
	Geum (n=22)	Han (n=55)	Geum (n=22)	Nakdong (n=33)	Geum (n=22)	Yeongsan (n=11)
Similarity (%)	35		38		28	
<i>C. demersum</i>	4 (18%)	11 (20%)	4 (18%)	19 (58%)	4 (18%)	3 (27%)
<i>H. verticillata</i>	11 (50%)	22 (40%)	11 (50%)	20 (61%)	11 (50%)	9 (82%)
<i>M. spicatum</i>	12 (55%)	42 (76%)	12 (55%)	24 (73%)	12 (55%)	4 (36%)
<i>N. marina</i>	4 (18%)	2 (4%)	4 (18%)	6 (18%)	4 (18%)	9 (82%)
<i>P. crispus</i>	10 (45%)	28 (51%)	10 (45%)	21 (64%)	10 (45%)	0 (0%)
<i>P. maackianus</i>	4 (18%)	15 (27%)	4 (18%)	2 (6%)	4 (18%)	1 (9%)
<i>P. malaianus</i>	6 (27%)	12 (22%)	6 (27%)	7 (21%)	6 (27%)	3 (27%)
<i>P. pusillus</i>	4 (18%)	4 (7%)	4 (18%)	0 (0%)	4 (18%)	0 (0%)
<i>V. natans</i>	6 (27%)	13 (24%)	6 (27%)	6 (18%)	6 (27%)	1 (9%)

Similarity (%)	Han River-Nakdong River		Han River-Yeongsan River		Nakdong River-Yeongsan River	
	Han (n=55)		Han (n=55)		Nakdong (n=33)	
	Han (n=55)	Nakdong (n=33)	Han (n=55)	Yeongsan (n=11)	Nakdong (n=33)	Yeongsan (n=11)
	42		25		34	
<i>C. demersum</i>	11 (20%)	19 (58%)	11 (20%)	3 (27%)	19 (58%)	3 (27%)
<i>H. verticillata</i>	22 (40%)	20 (61%)	22 (40%)	9 (82%)	20 (61%)	9 (82%)
<i>M. spicatum</i>	42 (76%)	24 (73%)	42 (76%)	4 (36%)	24 (73%)	4 (36%)
<i>N. marina</i>	2 (4%)	6 (18%)	2 (4%)	9 (82%)	6 (18%)	9 (82%)
<i>P. crispus</i>	28 (51%)	21 (64%)	28 (51%)	0 (0%)	21 (64%)	0 (0%)
<i>P. maackianus</i>	15 (27%)	2 (6%)	15 (27%)	1 (9%)	2 (6%)	1 (9%)
<i>P. malaianus</i>	12 (22%)	7 (21%)	12 (22%)	3 (27%)	7 (21%)	3 (27%)
<i>P. pusillus</i>	4 (7%)	0 (0%)	4 (7%)	0 (0%)	0 (0%)	0 (0%)
<i>V. natans</i>	13 (24%)	6 (18%)	13 (24%)	1 (9%)	6 (18%)	1 (9%)

Note: Geum, Geum River; Han, Han River; Nakdong, Nakdong River; Yeongsan, Yeongsan River. *C. demersum*, *Ceratophyllum demersum*; *H. verticillata*, *Hydrilla verticillata*; *M. spicatum*, *Myriophyllum spicatum*; *N. marina*, *Najas marina*; *P. crispus*, *Potamogeton crispus*; *P. malaianus*, *Potamogeton malaianus*; *P. maackianus*, *Potamogeton maackianus*; *P. pusillus*, *Potamogeton pusillus*; and *V. natans*, *Vallisneria natans*.

Appendix 2. Similarity percentage (SIMPER) analyses of environmental factors representing the mean and standard error between the four rivers. Environmental variables for SIMPER analysis were transformed with $\log(x + 1)$ to reduce the influence of high values, whereas mean and standard error were not transformed

Similarity (%)	Geum River-Han River		Geum River-Nakdong River		Geum River-Yeongsan River	
	Geum (n=22)		Geum (n=22)		Geum (n=22)	
	Han (n=55)		Nakdong (n=33)		Yeongsan (n=11)	
	80		82		79	
BOD [mg L ⁻¹]	2.47 ± 0.61	2.67 ± 0.27	2.47 ± 0.61	1.62 ± 0.12	2.47 ± 0.61	1.52 ± 0.20
Chla [mg m ⁻³]	11.6 ± 2.4	10.3 ± 0.8	11.6 ± 2.4	12.2 ± 1.6	11.6 ± 2.4	8.2 ± 1.9
NH4N [mg L⁻¹]	0.69 ± 0.32	1.23 ± 0.27	0.69 ± 0.32	0.17 ± 0.03	0.69 ± 0.32	0.13 ± 0.02
NO3N [mg L⁻¹]	2.09 ± 0.18	2.58 ± 0.14	2.09 ± 0.18	2.40 ± 0.14	2.09 ± 0.18	1.21 ± 0.17
SS [mg L ⁻¹]	7.82 ± 1.61	7.93 ± 0.60	7.82 ± 1.61	7.29 ± 0.51	7.82 ± 1.61	8.22 ± 1.16
TDP [mg L ⁻¹]	0.10 ± 0.05	0.09 ± 0.01	0.10 ± 0.05	0.04 ± 0.01	0.10 ± 0.05	0.04 ± 0.01
TN [mg L⁻¹]	3.74 ± 0.57	4.79 ± 0.44	3.74 ± 0.57	3.23 ± 0.23	3.74 ± 0.57	1.74 ± 0.22
TOC [mg L ⁻¹]	3.09 ± 0.51	3.48 ± 0.23	3.09 ± 0.51	2.77 ± 0.15	3.09 ± 0.51	2.64 ± 0.30
TP [mg L ⁻¹]	0.13 ± 0.07	0.12 ± 0.02	0.13 ± 0.07	0.06 ± 0.01	0.13 ± 0.07	0.06 ± 0.01
WD [m]	0.51 ± 0.06	0.68 ± 0.05	0.51 ± 0.06	0.62 ± 0.06	0.51 ± 0.06	0.61 ± 0.06

WV [m s ⁻¹]	0.06 ± 0.02	0.11 ± 0.03	0.06 ± 0.02	0.06 ± 0.02	0.06 ± 0.02	0.14 ± 0.04
Han River-Nakdong River						
Han River-Nakdong River			Han River-Yeongsan River		Nakdong River-Yeongsan River	
	Han (n=55)	Nakdong (n=33)	Han (n=55)	Yeongsan (n=11)	Nakdong (n=33)	Yeongsan (n=11)
Similarity (%)	83		79		82	
BOD [mg L ⁻¹]	2.67 ± 0.27	1.62 ± 0.12	2.67 ± 0.27	1.52 ± 0.20	1.62 ± 0.12	1.52 ± 0.20
Chla [mg m ⁻³]	10.3 ± 0.8	12.2 ± 1.6	10.3 ± 0.8	8.2 ± 1.9	12.2 ± 1.6	8.2 ± 1.9
NH4N [mg L⁻¹]	1.23 ± 0.27	0.17 ± 0.03	1.23 ± 0.27	0.13 ± 0.02	0.17 ± 0.03	0.13 ± 0.02
NO3N [mg L⁻¹]	2.58 ± 0.14	2.40 ± 0.14	2.58 ± 0.14	1.21 ± 0.17	2.40 ± 0.14	1.21 ± 0.17
SS [mg L ⁻¹]	7.93 ± 0.60	7.29 ± 0.51	7.93 ± 0.60	8.22 ± 1.16	7.29 ± 0.51	8.22 ± 1.16
TDP [mg L ⁻¹]	0.09 ± 0.01	0.04 ± 0.01	0.09 ± 0.01	0.04 ± 0.01	0.04 ± 0.01	0.04 ± 0.01
TN [mg L⁻¹]	4.79 ± 0.44	3.23 ± 0.23	4.79 ± 0.44	1.74 ± 0.22	3.23 ± 0.23	1.74 ± 0.22
TOC [mg L ⁻¹]	3.48 ± 0.23	2.77 ± 0.15	3.48 ± 0.23	2.64 ± 0.30	2.77 ± 0.15	2.64 ± 0.30
TP [mg L ⁻¹]	0.12 ± 0.02	0.06 ± 0.01	0.12 ± 0.02	0.06 ± 0.01	0.06 ± 0.01	0.06 ± 0.01
WD [m]	0.68 ± 0.05	0.62 ± 0.06	0.68 ± 0.05	0.61 ± 0.06	0.62 ± 0.06	0.61 ± 0.06
WV [m s ⁻¹]	0.11 ± 0.03	0.06 ± 0.02	0.11 ± 0.03	0.14 ± 0.04	0.06 ± 0.02	0.14 ± 0.04

Note: Significant differences in environmental factors between rivers were determined using the Mann-Whitney *U* test; bold text indicates significant differences ($p < 0.05$). BOD, biochemical oxygen demand; Chla, chlorophyll *a*; NH4N, ammonium nitrogen; NO3N, nitrate nitrogen; SS, suspended solids; TDP, total dissolved phosphorus; TN, total nitrogen; TOC, total organic carbon; TP, total phosphorus; WD, water depth; WV, water velocity.

Appendix 3. Locations of the 197 surveyed sites and submerged macrophytes coverage

Site	Latitude	Longitude	C.de	H.ve	M.sp	N.gr	N.ma	P.cr	P.ma	P.mc	P.ox	P.oc	P.pu	V.na
G-1	36.28440	127.35765	0	10	5	0	10	1	15	0	0	0	0	50
G-2	36.34643	127.35122	0	1	0	0	0	0	0	0	0	0	0	45
G-3	36.37105	127.37590	0	0	0	0	0	0	0	0	0	0	0	0
G-4	36.40542	127.41302	0	0	20	0	0	0	0	0	0	0	0	0
G-5	36.43735	127.39232	0	0	10	0	0	0	0	0	0	0	5	0
G-6	36.29598	127.45687	0	0	0	0	0	0	0	0	0	0	0	0
G-7	36.31618	127.43882	0	0	0	0	0	30	0	0	0	0	0	0
G-8	36.33845	127.41892	0	0	0	0	0	25	0	0	0	0	0	0
G-9	36.19258	127.38832	0	40	1	0	0	5	40	5	5	0	0	0
G-10	36.28688	127.37678	0	25	30	0	0	5	30	5	0	0	0	0
G-11	36.35323	127.40278	0	10	15	0	50	0	5	0	0	0	0	0
G-12	36.27610	126.89392	0	0	0	0	0	0	0	0	0	0	0	0
G-13	36.29360	127.14595	0	0	0	0	0	0	0	0	0	0	0	0
G-14	36.21012	127.08065	0	0	0	0	0	0	0	0	0	0	0	0
G-15	36.16185	127.02548	0	0	0	0	0	0	0	0	0	0	0	0
G-16	36.26125	127.06727	0	0	0	0	0	0	0	0	0	0	0	0
G-17	36.14612	127.03643	0	0	0	0	0	0	0	0	0	0	0	0
G-18	36.32463	126.87962	0	0	0	0	0	0	0	0	0	0	0	0
G-19	36.32725	126.90290	0	0	0	0	0	0	0	0	0	0	0	0

Site	Latitude	Longitude	C.de	H.ve	M.sp	N.gr	N.ma	P.cr	P.ma	P.mc	P.ox	P.oc	P.pu	V.na
G-20	36.33452	126.96612	0	0	0	0	0	0	0	0	0	0	0	0
G-21	36.46785	127.05395	0	0	0	0	0	0	0	0	0	0	0	0
G-22	35.55018	126.87363	0	70	0	0	0	0	0	0	0	0	0	0
G-23	35.67997	126.86302	0	0	0	0	0	0	0	0	0	0	0	0
G-24	35.67397	126.93608	0	0	0	0	0	0	0	0	0	0	0	0
G-25	35.71638	126.81768	0	0	0	0	0	0	0	0	0	0	0	0
G-26	35.75802	126.77927	0	0	0	0	0	0	0	0	0	0	0	0
G-27	35.76618	126.81307	0	0	0	0	0	0	0	0	0	0	0	0
G-28	35.80530	126.82652	0	1	0	0	0	0	0	0	0	0	0	0
G-29	35.83650	127.10540	70	0	0	0	0	1	0	0	0	0	1	0
G-30	35.87818	127.15478	40	20	0	0	60	0	0	0	0	0	5	30
G-31	35.97435	127.21663	1	20	1	0	0	40	60	15	0	0	0	1
G-32	35.85795	127.23997	0	80	0	0	0	0	0	0	0	0	0	0
G-33	35.91218	127.13958	15	10	0	0	5	10	0	5	0	0	0	60
G-34	35.87940	127.09663	0	0	0	0	0	0	0	0	0	0	0	0
G-35	35.93707	127.04885	0	0	0	0	0	5	0	0	0	0	5	0
G-36	35.90725	126.95733	0	0	0	0	0	0	0	0	0	0	0	0
G-37	35.87668	126.93848	0	0	0	0	0	0	0	0	0	0	0	0
G-38	36.45395	127.44045	0	0	10	0	0	1	0	0	0	0	0	0
G-39	36.46343	127.40167	0	0	5	0	0	0	0	0	0	0	0	0
G-40	36.51672	127.36475	0	0	5	0	0	0	1	0	0	0	0	0

Site	Latitude	Longitude	C.de	H.ve	M.sp	N.gr	N.ma	P.cr	P.ma	P.mc	P.ox	P.oc	P.pu	V.na
G-41	36.45255	127.15608	0	0	1	0	0	0	0	0	0	0	0	0
G-42	36.46683	127.13110	0	0	10	0	0	0	0	0	0	0	0	0
G-43	36.27610	126.89392	0	0	0	0	0	0	0	0	0	0	0	0
H-1	37.47788	126.93318	0	0	20	0	0	0	0	0	0	0	0	0
H-2	37.48753	126.89763	0	0	80	0	0	0	0	0	0	0	0	0
H-3	37.53955	126.88777	0	0	65	0	0	0	0	0	0	0	0	0
H-4	37.50723	126.87332	0	0	60	0	0	35	0	0	0	0	5	0
H-5	37.42680	126.89760	0	0	90	0	0	0	0	0	0	0	0	0
H-6	37.39733	126.93148	0	0	1	0	0	0	0	0	0	0	0	0
H-7	37.37373	126.94563	0	0	90	0	0	10	0	0	0	0	0	0
H-8	37.36595	126.95343	0	0	0	0	0	95	0	0	0	0	0	0
H-9	37.63482	127.06048	0	0	0	0	0	10	0	0	1	0	0	0
H-10	37.68782	127.04983	0	0	0	0	0	60	0	0	5	0	0	0
H-11	37.71520	127.05063	0	0	0	0	0	15	0	0	5	0	0	0
H-12	37.73515	127.05405	0	0	0	0	0	0	0	0	0	0	0	0
H-13	37.76678	127.04633	0	0	0	0	0	0	0	0	0	0	0	0
H-14	37.46805	127.12305	0	0	50	0	0	0	0	0	0	0	0	0
H-15	37.44192	127.11832	0	0	25	0	0	0	0	0	0	0	0	0
H-16	37.42923	127.11710	0	0	30	0	0	0	0	0	0	0	0	0
H-17	37.35520	127.11430	0	0	0	0	0	0	0	0	0	0	0	0
H-18	37.34140	127.11688	0	0	0	0	0	0	0	0	0	0	0	0

Site	Latitude	Longitude	C.de	H.ve	M.sp	N.gr	N.ma	P.cr	P.ma	P.mc	P.ox	P.oc	P.pu	V.na
H-19	37.38608	127.11708	0	0	15	0	0	0	0	0	0	0	0	0
H-20	37.85190	127.67778	0	1	10	0	0	1	0	60	0	10	0	5
H-21	37.85200	127.67748	0	5	15	0	0	5	60	10	0	0	0	0
H-22	37.86683	127.68224	0	1	10	1	0	0	0	5	0	30	0	50
H-23	37.85428	127.68166	0	1	1	0	0	0	0	30	0	40	0	30
H-24	37.89662	127.70457	0	40	5	0	0	0	0	30	0	20	0	0
H-25	37.18495	127.00525	0	0	0	0	0	0	0	0	0	0	0	0
H-26	37.12358	126.99925	5	0	0	0	0	0	0	0	0	0	1	0
H-27	37.84513	127.02722	0	0	0	0	0	0	0	0	0	0	0	0
H-28	37.10110	127.03987	0	0	10	0	0	0	0	0	0	0	0	0
H-29	37.13443	127.05918	0	0	1	0	0	0	0	0	0	0	0	0
H-30	37.15875	127.07300	0	0	1	0	0	0	0	0	0	0	0	0
H-31	37.17860	127.08460	5	0	10	0	0	0	0	0	0	0	0	0
H-32	37.19243	127.08260	0	0	1	0	0	30	0	0	0	0	0	0
H-33	37.09813	127.08418	0	10	5	0	0	0	0	0	0	0	20	0
H-34	37.10698	127.13393	0	5	0	0	0	0	0	0	0	0	50	0
H-35	37.41933	127.28070	0	0	0	0	0	0	0	0	0	0	0	0
H-36	37.40657	127.26275	0	0	0	0	0	0	0	0	0	0	0	0
H-37	37.37022	127.24032	0	0	0	0	0	0	0	0	0	0	0	0
H-38	37.33718	127.24835	0	0	0	0	0	0	0	0	0	0	0	0
H-39	37.27852	127.22277	0	0	0	0	0	0	0	0	0	0	0	0

Site	Latitude	Longitude	C.de	H.ve	M.sp	N.gr	N.ma	P.cr	P.ma	P.mc	P.ox	P.oc	P.pu	V.na
H-40	37.09550	127.47658	0	0	0	0	0	0	0	0	0	0	0	0
H-41	37.11845	127.63345	0	0	0	0	0	0	0	0	0	0	0	0
H-42	37.20213	127.71875	0	0	0	0	0	0	0	0	0	0	0	0
H-43	37.33295	127.53535	0	0	0	0	0	0	0	0	0	0	0	0
H-44	37.23748	127.44833	0	0	0	0	0	0	0	0	0	0	0	0
H-45	37.46597	127.52802	0	0	1	0	0	0	0	0	0	0	0	0
H-46	37.58898	127.22480	0	0	0	0	0	15	0	0	0	0	0	0
H-47	37.69145	127.16360	0	0	60	0	0	0	0	0	0	0	0	0
H-48	37.66215	127.14993	5	15	10	0	0	1	60	0	0	0	0	0
H-49	37.61553	127.14743	1	0	50	0	0	0	0	0	0	0	0	0
H-50	37.24328	127.74827	5	30	1	0	50	5	20	0	0	0	0	1
H-51	37.30547	127.80895	0	0	50	0	0	5	20	0	0	0	0	0
H-52	37.36053	127.83368	0	0	10	0	0	10	3	0	0	0	0	0
H-53	37.34150	127.96372	0	0	0	0	0	5	0	0	0	0	0	0
H-54	38.10230	127.70770	0	40	30	0	0	0	0	5	0	0	0	0
H-55	37.92202	127.71762	0	40	30	0	0	0	0	10	0	0	0	5
H-56	37.87068	127.72098	0	0	20	0	0	30	0	0	0	0	0	0
H-57	37.84418	127.53918	50	50	0	0	0	0	0	10	0	15	0	5
H-58	37.01437	127.91558	0	15	25	0	0	0	0	0	0	0	0	0
H-59	37.06957	127.88555	0	30	0	0	0	5	20	0	0	0	0	0
H-60	37.25177	127.68540	0	15	25	0	0	0	0	5	0	0	0	1

Site	Latitude	Longitude	C.de	H.ve	M.sp	N.gr	N.ma	P.cr	P.ma	P.mc	P.ox	P.oc	P.pu	V.na
H-61	37.29775	127.65040	0	0	0	0	0	0	25	0	0	0	0	25
H-62	37.48500	127.48797	1	50	1	0	0	1	5	5	0	0	0	50
H-63	37.46577	127.49332	20	80	1	0	0	0	5	10	0	0	0	60
H-64	37.41170	127.53888	0	0	10	0	0	5	10	40	0	0	0	0
H-65	37.42997	127.53148	10	60	10	0	10	1	0	0	0	0	0	50
H-66	37.39267	127.54082	0	10	5	0	0	1	20	0	0	0	0	0
H-67	37.38893	127.54497	0	0	1	0	0	0	0	0	0	0	0	0
H-68	37.36483	127.56107	0	70	10	0	0	5	0	10	0	0	0	30
H-69	37.88162	127.68977	0	90	1	0	0	5	0	1	0	0	0	0
H-70	37.87844	127.68351	90	0	0	0	0	0	0	0	0	0	0	0
H-71	37.90497	127.71078	10	5	0	0	0	80	0	0	0	0	0	20
N-1	35.55053	129.35087	0	0	0	0	0	0	0	0	0	0	0	0
N-2	35.55240	129.27608	40	40	0	0	0	0	50	0	0	0	0	0
N-3	35.56148	129.24918	0	0	0	0	0	0	0	0	0	0	0	0
N-4	35.58575	129.23142	0	0	0	0	0	0	0	0	0	0	0	0
N-5	35.56543	129.19567	0	40	30	0	0	30	0	0	0	0	0	0
N-6	35.54752	129.15077	0	30	70	0	0	0	0	0	0	0	0	0
N-7	35.98107	128.90065	0	30	0	0	0	1	0	30	0	0	0	40
N-8	35.92328	128.85838	0	1	0	0	0	10	10	0	30	0	0	40
N-9	35.89703	128.80173	5	30	10	0	5	10	5	0	25	0	0	50
N-10	35.85735	128.68775	10	5	5	0	0	0	5	0	0	0	0	80

Site	Latitude	Longitude	C.de	H.ve	M.sp	N.gr	N.ma	P.cr	P.ma	P.mc	P.ox	P.oc	P.pu	V.na
N-11	35.88930	128.63787	0	0	0	0	0	0	0	0	0	0	0	0
N-12	35.89618	128.54972	0	10	1	0	0	0	0	0	0	0	0	30
N-13	36.11842	128.13085	40	15	0	0	0	5	0	0	0	0	0	0
N-14	36.22800	128.30800	30	0	0	0	0	5	0	0	0	0	0	0
N-15	36.41173	128.24613	5	30	50	0	10	0	0	0	0	0	0	0
N-16	36.52890	128.36363	0	0	0	0	0	0	0	0	0	0	0	0
N-17	36.53777	128.46558	1	10	20	0	0	10	0	0	0	0	0	0
N-18	36.53907	128.65720	30	10	5	0	0	20	0	0	0	0	0	0
N-19	36.54938	128.70147	0	0	0	0	0	0	0	0	0	0	0	0
N-20	36.71919	128.64610	0	10	20	0	0	30	0	0	0	0	0	0
N-21	36.73035	128.61972	5	0	0	0	0	0	0	0	0	0	0	0
N-22	36.73675	128.56990	0	0	0	0	0	0	0	0	0	0	0	0
N-23	36.61653	128.48753	0	0	0	0	0	0	0	0	0	0	0	0
N-24	36.60173	128.41742	0	0	0	0	0	0	0	0	0	0	0	0
N-25	36.62230	128.29295	0	0	0	0	0	0	0	0	0	0	0	0
N-26	36.59322	128.21067	0	20	10	0	30	5	10	50	0	0	0	0
N-27	36.53677	128.21265	0	0	0	0	0	0	0	0	0	0	0	0
N-28	36.53520	128.25048	0	0	0	0	0	0	0	0	0	0	0	0
N-29	35.37138	128.64660	0	0	0	0	0	0	0	0	0	0	0	0
N-30	35.38258	128.47412	0	0	0	0	0	0	0	0	0	0	0	0
N-31	35.61305	128.35810	0	0	20	0	10	10	10	0	0	0	0	10

Site	Latitude	Longitude	C.de	H.ve	M.sp	N.gr	N.ma	P.cr	P.ma	P.mc	P.ox	P.oc	P.pu	V.na
N-32	35.75097	128.38707	0	10	20	0	0	0	0	0	0	0	0	0
N-33	35.88243	128.38693	5	0	10	0	10	10	0	0	0	0	0	0
N-34	36.00367	128.39302	1	0	5	0	0	1	0	0	0	0	0	0
N-35	36.08538	128.39710	5	60	10	0	5	5	0	0	0	0	0	0
N-36	36.19423	128.36373	10	0	20	0	0	10	10	0	0	0	0	0
N-37	36.27338	128.34483	0	0	10	0	0	10	0	0	0	0	0	0
N-38	36.41077	128.26408	10	10	20	0	0	10	0	0	0	0	0	0
N-39	36.42485	128.23675	10	10	10	0	0	10	0	0	0	0	0	0
N-40	36.45588	128.25830	1	0	1	0	0	0	0	0	0	0	0	0
N-41	36.56258	128.29675	5	0	0	0	0	1	0	0	0	0	0	0
N-42	36.53848	128.46848	1	1	0	0	0	1	0	0	0	0	0	0
N-43	36.56055	128.56980	0	40	1	0	0	1	0	0	0	0	0	0
N-44	36.41157	128.24848	0	0	40	0	0	0	0	0	0	0	0	0
N-45	36.41160	128.26738	0	0	60	0	0	0	0	0	0	0	0	0
N-46	36.40308	128.30080	0	0	30	0	0	0	0	0	0	0	0	0
S-1	35.06317	127.74185	0	0	0	0	0	0	0	0	0	0	0	0
S-2	35.13468	127.69075	0	0	0	0	0	0	0	0	0	0	0	0
S-3	35.18468	127.62172	0	0	0	0	0	0	0	0	0	0	0	0
S-4	35.18973	127.54522	0	60	30	0	0	0	1	0	0	0	0	0
S-5	35.19868	127.47417	0	5	0	0	0	0	0	0	0	0	0	0
S-6	35.19508	127.37627	0	70	0	0	0	1	0	0	0	0	0	0

Site	Latitude	Longitude	C.de	H.ve	M.sp	N.gr	N.ma	P.cr	P.ma	P.mc	P.ox	P.oc	P.pu	V.na
S-7	35.29390	127.32900	0	5	0	0	0	0	0	0	0	0	0	0
S-8	35.31123	127.29530	0	80	0	0	0	1	0	0	0	0	0	0
S-9	35.34643	127.18745	0	5	0	0	0	0	0	0	0	0	0	0
S-10	35.44102	127.20383	0	60	0	0	0	60	0	0	0	0	0	0
Y-1	35.15957	127.34507	5	70	0	0	20	0	0	0	0	0	0	0
Y-2	35.13033	127.25858	20	70	0	0	20	0	1	0	0	50	0	5
Y-3	35.18343	127.09333	0	0	0	0	0	0	0	0	0	0	0	0
Y-4	35.13327	127.10053	0	0	0	0	0	0	0	0	0	0	0	0
Y-5	35.04243	127.12232	0	30	0	0	70	0	0	0	0	0	0	0
Y-6	34.83143	127.14705	0	0	0	0	0	0	0	0	0	0	0	0
Y-7	34.75968	127.02495	0	0	0	0	0	0	0	0	0	0	0	0
Y-8	34.72608	126.90698	1	50	0	0	0	0	10	5	5	0	0	0
Y-9	34.65482	126.88828	5	30	0	0	20	0	50	0	0	0	0	0
Y-10	34.63665	126.81260	0	60	0	0	40	0	0	0	0	0	0	0
Y-11	34.68713	126.85493	0	0	0	0	0	0	0	0	0	0	0	0
Y-12	34.79633	126.83053	0	0	0	0	0	0	0	0	0	0	0	0
Y-13	34.84298	126.87618	0	0	0	0	0	0	0	0	0	0	0	0
Y-14	35.32453	126.98392	0	0	20	0	0	0	0	0	0	0	0	0
Y-15	35.31620	126.97457	0	70	2	0	10	0	0	0	0	0	0	0
Y-16	35.29890	126.95518	0	30	30	0	5	0	0	0	0	0	0	0
Y-17	35.24158	126.88742	0	0	5	0	0	0	0	0	0	0	0	0

Site	Latitude	Longitude	C.de	H.ve	M.sp	N.gr	N.ma	P.cr	P.ma	P.mc	P.ox	P.oc	P.pu	V.na
Y-18	35.21710	126.85758	0	0	0	0	5	0	0	0	0	0	0	0
Y-19	35.18658	126.85742	0	0	0	0	0	0	0	0	0	0	0	0
Y-20	35.14073	126.82707	0	0	0	0	0	0	0	0	0	0	0	0
Y-21	35.10933	126.81948	0	0	0	0	0	0	0	0	0	0	0	0
Y-22	35.07293	126.78470	0	0	0	0	0	0	0	0	0	0	0	0
Y-23	35.02447	126.73922	0	0	0	0	0	0	0	0	0	0	0	0
Y-24	35.00242	126.70987	0	0	0	0	0	0	0	0	0	0	0	0
Y-25	34.98472	126.64190	0	0	0	0	0	0	0	0	0	0	0	0
Y-26	34.99183	126.59373	0	0	0	0	0	0	0	0	0	0	0	0
Y-27	34.91828	126.51027	0	0	0	0	0	0	0	0	0	0	0	0

Note: H, Han River; G, Geum River; N, Nakdong River; S, Seomjin River; Y, Yeongsan River, C.de, *Ceratophyllum demersum* 붕어마름; H.ve, *Hydrilla verticillata* 검정말; M.sp, *Myriophyllum spicatum*, 이삭물수세미; N.gr, *Najas graminea* 나자스말; N.ma, *N. marina* 민나자스말; P.cr, *Potamogeton crispus* 말즘; P.ma, *P. malainus* 대가래; P.mc, *P. maackianus* 새우가래; P.oc *P. octandrus* 애기가래; P.ox, *P. oxyphyllus* 말; P.pu, *P. pusillus* 싹말, and V.na, *Vallisneria natans* 나사말.

Appendix 4. Water environmental factors at the 197 surveyed sites

Sites	BOD	Chla	NH ₄ N	NO ₃ N	SS	TDP	TN	TOC	TP	WD	WT	WV	Substratum
G-1	1.39	7.20	0.05	1.40	3.94	0.02	2.11	1.72	0.03	0.50	23.2	0.02	fines
G-2	1.50	6.16	0.10	1.53	4.68	0.03	2.27	1.95	0.04	0.80	22.3	0.00	boulder
G-3	1.77	7.31	0.09	1.40	5.15	0.03	2.25	2.01	0.05	0.80	23.0	0.00	cobble
G-4	4.97	11.12	2.48	3.97	5.82	0.15	8.82	5.12	0.21	0.60	25.0	0.33	cobble
G-5	3.78	12.33	1.72	4.70	4.64	0.10	8.54	4.88	0.14	0.40	25.0	0.00	fines
G-6	1.04	3.75	0.08	3.10	2.43	0.02	3.60	1.31	0.03	0.30	22.0	0.00	pebble
G-7	1.44	5.63	0.05	2.30	3.41	0.02	3.15	1.67	0.03	0.35	24.5	0.00	pebble
G-8	1.92	6.07	0.22	2.29	3.87	0.05	3.60	1.90	0.07	0.25	23.7	0.05	cobble
G-9	1.02	3.53	0.04	1.85	1.81	0.02	2.33	1.14	0.02	0.30	22.2	0.00	pebble
G-10	1.24	4.78	0.06	1.67	2.22	0.02	2.28	1.31	0.03	0.55	22.8	0.02	boulder
G-11	1.85	7.95	0.15	1.56	2.88	0.03	2.52	1.75	0.04	0.40	24.1	0.08	pebble
G-12	2.34	29.77	0.40	2.05	15.77	0.03	3.16	3.74	0.07	0.50	23.4	0.02	fines
G-13	2.01	8.79	0.07	1.81	10.85	0.04	2.29	3.32	0.08	0.90	25.0	0.00	boulder
G-14	1.90	8.98	0.22	1.66	14.63	0.06	2.36	3.04	0.08	0.40	23.5	0.05	boulder
G-15	4.74	36.50	1.40	3.24	29.98	0.17	5.92	5.78	0.26	0.90	24.2	0.00	boulder
G-16	4.81	9.46	0.66	2.57	17.28	0.50	4.06	5.10	0.57	0.55	24.2	0.05	fines
G-17	6.17	35.76	1.11	3.19	26.16	0.16	5.56	6.26	0.21	0.90	25.0	0.00	boulder
G-18	1.75	6.37	0.05	1.92	3.17	0.03	2.32	2.95	0.04	0.30	25.4	0.27	cobble
G-19	1.74	11.82	0.15	1.77	25.67	0.04	2.37	3.28	0.06	0.25	23.3	0.30	fines

Sites	BOD	Chla	NH ₄ N	NO ₃ N	SS	TDP	TN	TOC	TP	WD	WT	WV	Substratum
G-20	2.83	39.25	0.33	2.23	12.59	0.04	3.28	4.50	0.07	0.70	22.9	0.00	fines
G-21	1.34	8.16	0.05	1.58	8.06	0.02	1.97	2.04	0.03	0.20	24.0	0.11	cobble
G-22	0.90	3.06	0.03	1.42	3.24	0.01	1.87	1.24	0.02	0.25	22.4	0.38	pebble
G-23	2.68	13.21	0.60	2.86	20.27	0.07	4.62	5.60	0.12	0.70	22.4	0.00	fines
G-24	2.44	7.30	0.07	2.19	16.61	0.08	2.96	3.99	0.09	1.20	20.6	0.00	cobble
G-25	2.55	22.65	0.42	2.30	22.92	0.06	3.36	4.86	0.10	1.10	22.9	0.00	boulder
G-26	3.48	26.54	0.45	2.06	35.59	0.07	3.81	6.83	0.13	0.80	23.6	0.00	fines
G-27	3.65	26.11	0.39	1.89	27.80	0.05	3.36	5.64	0.12	0.90	25.1	0.00	fines
G-28	5.06	45.35	1.32	2.49	22.87	0.12	5.79	6.43	0.23	0.90	24.4	0.00	fines
G-29	2.34	7.73	0.20	1.82	11.73	0.06	2.60	2.68	0.08	0.30	24.4	0.08	fines
G-30	1.38	4.70	0.07	2.74	8.33	0.03	3.70	1.71	0.03	0.50	24.1	0.00	pebble
G-31	1.05	2.60	0.08	1.55	2.20	0.02	2.18	1.88	0.03	0.50	20.5	0.08	cobble
G-32	0.80	2.47	0.06	2.35	2.34	0.02	2.99	0.94	0.02	0.35	23.1	0.16	pebble
G-33	1.66	16.76	0.05	1.61	7.95	0.07	2.08	3.02	0.08	1.30	23.0	0.00	cobble
G-34	6.88	18.63	4.25	2.03	8.79	0.41	7.55	9.25	0.51	0.97	23.4	0.00	pebble
G-35	14.32	23.38	7.03	1.53	31.61	1.26	12.15	11.77	1.51	0.20	25.1	0.08	fines
G-36	4.72	43.50	1.80	2.08	22.17	0.22	4.73	6.99	0.28	1.00	23.9	0.00	cobble
G-37	9.79	56.14	2.50	3.83	32.68	0.13	8.78	9.17	0.21	1.20	26.0	0.05	boulder
G-38	0.61	3.45	0.04	1.17	3.45	0.01	1.51	2.52	0.02	0.78	17.9	0.00	pebble
G-39	0.61	3.45	0.04	1.17	3.45	0.01	1.51	2.52	0.02	0.60	17.9	0.00	pebble
G-40	1.93	12.28	0.46	2.36	8.22	0.04	3.45	3.94	0.06	0.20	20.0	0.05	cobble

Sites	BOD	Chla	NH ₄ N	NO ₃ N	SS	TDP	TN	TOC	TP	WD	WT	WV	Substratum
G-41	2.31	32.81	0.47	2.20	16.64	0.03	3.44	3.94	0.08	0.70	22.4	0.00	pebble
G-42	2.31	32.81	0.47	2.20	16.64	0.03	3.44	3.94	0.08	0.50	22.4	0.00	finest
G-43	2.44	33.92	0.47	2.22	17.49	0.03	3.43	3.89	0.08	0.95	22.9	0.00	pebble
H-1	2.13	9.38	0.38	2.80	2.88	0.15	4.16	2.73	0.17	0.45	21.8	0.00	boulder
H-2	2.13	9.38	0.38	2.80	2.88	0.15	4.16	2.73	0.17	0.50	21.8	0.00	finest
H-3	4.73	13.79	4.44	4.18	10.22	0.13	11.80	5.03	0.16	0.50	23.6	0.03	boulder
H-4	6.22	10.65	8.23	4.32	9.19	0.15	15.05	6.66	0.24	0.40	24.7	0.22	finest
H-5	7.15	6.56	7.37	3.75	6.72	0.14	13.34	6.20	0.16	0.60	24.1	0.90	boulder
H-6	4.06	14.88	4.22	2.93	8.25	0.07	8.79	4.77	0.08	0.15	23.8	0.30	finest
H-7	3.82	4.79	6.28	3.00	4.16	0.07	11.18	5.71	0.09	0.40	23.6	0.36	finest
H-8	3.44	3.17	6.53	2.68	4.13	0.08	10.78	5.41	0.10	0.30	23.6	0.38	pebble
H-9	2.74	6.71	1.03	4.93	9.53	0.13	7.90	3.53	0.17	0.15	23.8	0.36	finest
H-10	4.77	5.95	1.88	5.00	14.73	0.12	8.48	5.39	0.23	0.50	23.9	0.30	finest
H-11	1.99	5.95	0.28	3.78	10.23	0.08	4.78	4.44	0.10	0.20	21.4	0.50	cobble
H-12	1.99	5.95	0.28	3.78	10.23	0.08	4.78	4.44	0.10	0.35	21.4	0.58	finest
H-13	1.99	5.95	0.28	3.78	10.23	0.08	4.78	4.44	0.10	0.50	21.4	0.16	finest
H-14	6.93	7.45	3.33	3.32	12.78	0.34	8.04	6.54	0.44	1.20	24.8	0.00	boulder
H-15	3.86	13.67	1.01	2.85	7.59	0.14	4.75	4.56	0.15	0.50	24.1	0.72	cobble
H-16	3.86	13.67	1.01	2.85	7.59	0.14	4.75	4.56	0.15	0.66	24.1	0.00	cobble
H-17	7.59	10.86	1.62	2.90	12.36	0.22	5.74	5.43	0.25	0.35	24.8	0.14	pebble
H-18	7.59	10.86	1.62	2.90	12.36	0.22	5.74	5.43	0.25	0.40	24.8	0.63	pebble

Sites	BOD	Chla	NH ₄ N	NO ₃ N	SS	TDP	TN	TOC	TP	WD	WT	WV	Substratum
H-19	7.59	10.86	1.62	2.90	12.36	0.22	5.74	5.43	0.25	0.36	24.8	0.05	boulder
H-20	1.24	6.58	0.09	1.37	3.74	0.01	2.04	1.83	0.02	0.94	18.9	0.00	fines
H-21	1.24	6.58	0.09	1.37	3.74	0.01	2.04	1.83	0.02	0.99	18.9	0.00	fines
H-22	1.24	6.58	0.09	1.37	3.74	0.01	2.04	1.83	0.02	0.70	18.9	0.00	fines
H-23	1.24	6.58	0.09	1.37	3.74	0.01	2.04	1.83	0.02	0.90	18.9	0.00	fines
H-24	1.24	6.58	0.09	1.37	3.74	0.01	2.04	1.83	0.02	1.50	18.9	0.00	cobble
H-25	8.88	16.67	3.65	4.03	13.28	0.60	10.08	7.78	0.74	1.20	25.2	0.05	boulder
H-26	7.01	27.20	3.43	4.09	16.59	0.52	9.73	7.80	0.67	0.30	25.5	0.00	fines
H-27	6.83	45.41	2.32	3.14	17.25	0.23	6.93	6.94	0.28	1.20	24.2	0.02	fines
H-28	7.90	32.26	2.95	3.24	16.30	0.41	7.97	6.73	0.46	0.67	24.6	0.02	fines
H-29	6.68	14.50	4.20	3.92	15.42	0.44	9.50	6.80	0.55	0.40	25.3	0.11	fines
H-30	2.73	19.66	0.64	4.10	22.50	0.12	6.00	4.62	0.20	1.00	24.7	0.02	fines
H-31	3.24	25.77	0.71	3.98	18.12	0.13	5.97	4.65	0.17	0.40	23.8	0.00	fines
H-32	3.28	23.42	0.68	4.77	12.82	0.15	7.00	4.93	0.18	0.60	24.1	0.19	cobble
H-33	2.09	10.91	0.34	1.59	7.68	0.05	2.55	3.75	0.07	0.30	22.5	0.08	fines
H-34	1.56	7.09	0.09	1.40	6.30	0.02	2.05	3.03	0.05	0.25	23.7	0.22	pebble
H-35	2.57	29.27	0.73	3.09	13.21	0.03	4.61	2.82	0.06	0.25	22.8	0.49	pebble
H-36	3.19	42.38	0.86	3.18	14.07	0.04	4.85	2.90	0.07	0.40	23.4	0.27	pebble
H-37	3.72	32.24	1.49	3.23	12.75	0.03	5.99	4.35	0.08	0.50	23.0	0.02	fines
H-38	3.31	27.93	2.20	3.51	11.15	0.05	6.70	3.13	0.07	0.25	23.0	0.24	fines
H-39	2.92	26.30	0.33	1.87	10.24	0.05	2.88	2.66	0.08	0.35	23.8	0.00	fines

Sites	BOD	Chla	NH ₄ N	NO ₃ N	SS	TDP	TN	TOC	TP	WD	WT	WV	Substratum
H-40	3.47	24.22	0.45	2.82	11.23	0.11	4.24	4.26	0.14	0.60	22.3	0.11	fines
H-41	3.36	32.38	0.38	2.52	12.28	0.08	3.65	4.00	0.10	0.50	23.3	0.16	cobble
H-42	2.92	29.10	0.28	2.55	17.06	0.06	3.57	4.02	0.12	0.65	22.1	0.16	fines
H-43	4.15	10.36	2.74	3.76	12.19	0.12	7.70	3.49	0.13	0.80	25.3	0.83	boulder
H-44	5.49	11.60	2.32	2.71	11.15	0.16	6.25	4.44	0.19	0.70	24.5	0.22	boulder
H-45	1.23	6.15	0.06	1.89	7.19	0.02	2.34	1.92	0.03	0.50	23.5	0.11	cobble
H-46	1.35	5.51	0.12	2.73	3.15	0.09	3.28	1.79	0.08	0.25	20.4	0.22	pebble
H-47	1.50	6.88	0.09	2.42	4.06	0.03	3.08	3.39	0.03	0.90	21.9	0.00	fines
H-48	1.85	18.75	0.07	3.00	6.13	0.03	3.74	3.54	0.04	0.43	22.6	0.27	pebble
H-49	4.86	20.74	2.20	3.13	8.92	0.09	6.69	5.67	0.12	0.30	23.2	0.22	fines
H-50	1.75	13.29	0.48	2.10	8.56	0.07	3.17	2.92	0.09	0.70	22.8	0.00	cobble
H-51	1.80	10.97	0.41	2.34	7.72	0.07	3.83	2.97	0.10	0.50	23.5	0.30	fines
H-52	2.08	9.82	0.68	2.48	5.81	0.10	4.38	3.29	0.13	0.70	22.9	0.05	cobble
H-53	1.58	7.21	0.20	2.98	10.56	0.04	4.34	2.67	0.07	0.80	21.7	0.05	fines
H-54	0.87	2.13	0.06	2.50	3.42	0.01	3.42	1.56	0.02	1.10	23.5	0.02	boulder
H-55	1.10	3.84	0.06	1.11	2.68	0.01	1.77	1.82	0.02	1.30	19.6	0.02	cobble
H-56	1.43	5.39	0.13	2.59	5.97	0.03	3.67	2.29	0.05	0.60	21.6	0.02	fines
H-57	0.99	6.90	0.06	1.35	4.02	0.01	1.71	1.92	0.02	0.50	18.7	0.00	fines
H-58	0.87	3.35	0.07	2.01	2.65	0.02	2.64	2.05	0.03	1.05	17.7	0.08	fines
H-59	0.99	3.88	0.08	1.96	4.12	0.02	2.68	2.33	0.03	0.60	19.7	0.05	fines
H-60	1.11	7.32	0.07	1.77	6.18	0.03	2.33	2.03	0.04	0.80	22.0	0.00	cobble

Sites	BOD	Chla	NH ₄ N	NO ₃ N	SS	TDP	TN	TOC	TP	WD	WT	WV	Substratum
H-61	0.92	7.07	0.06	1.75	7.16	0.03	2.24	1.74	0.04	1.20	22.2	0.00	cobble
H-62	1.65	12.92	0.08	1.90	8.84	0.02	2.43	2.49	0.05	0.52	22.8	0.00	cobble
H-63	1.65	12.92	0.08	1.90	8.84	0.02	2.43	2.49	0.05	1.05	22.8	0.00	finer
H-64	1.60	11.00	0.14	1.99	10.77	0.03	2.61	2.55	0.06	1.20	22.4	0.00	boulder
H-65	1.60	11.00	0.14	1.99	10.77	0.03	2.61	2.55	0.06	0.60	22.4	0.00	pebble
H-66	1.60	11.00	0.14	1.99	10.77	0.03	2.61	2.55	0.06	1.05	22.4	0.00	boulder
H-67	1.60	11.00	0.14	1.99	10.77	0.03	2.61	2.55	0.06	1.20	22.4	0.00	boulder
H-68	1.07	7.75	0.05	1.67	8.05	0.03	2.15	1.80	0.04	0.60	23.8	0.00	finer
H-69	1.24	6.58	0.09	1.37	3.74	0.01	2.04	1.83	0.02	0.78	18.9	0.00	finer
H-70	1.24	6.58	0.09	1.37	3.74	0.01	2.04	1.83	0.02	1.60	18.9	0.00	finer
H-71	1.24	6.58	0.09	1.37	3.74	0.01	2.04	1.83	0.02	0.97	18.9	0.00	finer
N-1	1.22	5.10	0.12	1.40	8.52	0.06	1.88	2.04	0.07	0.70	23.6	0.05	finer
N-2	1.19	9.66	0.53	2.27	4.08	0.03	3.34	2.26	0.05	0.35	23.2	0.00	boulder
N-3	0.95	12.63	0.03	2.43	5.12	0.03	2.85	1.68	0.05	0.35	23.2	0.16	cobble
N-4	0.64	4.28	0.03	2.70	1.07	0.06	3.06	1.56	0.07	0.40	23.8	0.13	cobble
N-5	1.27	4.14	0.43	3.12	1.61	0.20	4.04	2.52	0.22	0.90	22.9	0.02	pebble
N-6	0.61	2.70	0.03	2.53	1.19	0.03	2.90	1.51	0.04	0.30	22.0	0.00	cobble
N-7	1.38	7.71	0.24	2.64	6.52	0.04	6.10	4.08	0.07	0.60	23.2	0.00	cobble
N-8	1.77	11.89	0.24	2.64	8.20	0.04	3.43	4.28	0.06	0.50	24.0	0.11	pebble
N-9	1.90	8.99	0.24	2.64	12.95	0.04	3.67	3.47	0.05	0.40	24.8	0.11	pebble
N-10	3.00	14.35	0.24	2.64	13.56	0.04	5.07	4.81	0.10	0.60	23.6	0.00	pebble

Sites	BOD	Chla	NH ₄ N	NO ₃ N	SS	TDP	TN	TOC	TP	WD	WT	WV	Substratum
N-11	2.52	13.02	0.43	3.67	6.01	0.04	6.25	4.41	0.06	0.90	24.1	0.00	cobble
N-12	3.74	40.27	0.33	5.88	10.74	0.12	8.61	4.65	0.17	0.25	25.1	0.08	finer
N-13	0.76	3.81	0.11	2.73	6.09	0.03	3.21	1.44	0.09	0.25	24.3	0.08	finer
N-14	1.03	4.97	0.11	3.12	10.92	0.05	3.62	2.02	0.12	0.35	25.2	0.15	finer
N-15	1.75	14.34	0.05	1.88	6.46	0.02	2.37	2.83	0.04	0.50	23.9	0.00	boulder
N-16	0.93	3.32	0.13	1.80	6.19	0.01	2.17	2.40	0.02	0.32	23.3	0.08	pebble
N-17	0.95	3.42	0.13	1.76	6.02	0.01	2.18	2.53	0.02	0.30	21.5	0.30	finer
N-18	1.29	5.19	0.04	2.74	6.10	0.02	3.38	2.94	0.03	0.60	23.9	0.05	pebble
N-19	0.86	4.49	0.10	1.43	3.08	0.01	1.83	2.52	0.02	0.70	20.2	0.00	boulder
N-20	0.82	4.99	0.10	2.45	11.06	0.03	2.84	1.30	0.04	0.25	23.1	0.16	cobble
N-21	1.75	3.02	0.61	3.55	3.72	0.04	4.85	1.77	0.05	0.30	25.4	0.58	finer
N-22	1.03	5.40	0.16	3.40	16.04	0.05	3.78	2.80	0.09	0.10	23.4	0.30	finer
N-23	0.90	3.52	0.10	3.49	7.71	0.04	3.83	1.34	0.05	0.20	24.7	0.44	finer
N-24	1.24	4.77	0.14	2.16	6.42	0.05	2.75	2.09	0.06	0.20	24.3	0.47	finer
N-25	1.23	6.92	0.05	3.06	28.01	0.05	2.65	2.95	0.13	0.10	22.9	0.28	finer
N-26	1.02	2.29	0.04	1.64	2.03	0.01	2.05	1.25	0.03	0.80	23.7	0.00	cobble
N-27	1.56	3.63	0.07	1.64	9.53	0.02	2.08	2.02	0.04	0.13	22.8	0.33	finer
N-28	1.30	5.41	0.07	1.70	3.10	0.02	2.18	1.52	0.03	0.25	24.7	0.00	cobble
N-29	2.28	31.14	0.08	2.09	12.57	0.03	2.89	3.82	0.07	0.75	24.3	0.02	finer
N-30	2.31	28.82	0.07	1.98	11.07	0.03	2.65	2.63	0.06	1.03	25.1	0.00	finer
N-31	2.37	28.56	0.08	2.38	10.37	0.04	3.22	3.15	0.07	0.87	25.0	0.00	pebble

Sites	BOD	Chla	NH ₄ N	NO ₃ N	SS	TDP	TN	TOC	TP	WD	WT	WV	Substratum
N-32	2.72	32.17	0.18	2.82	10.92	0.04	3.60	3.35	0.06	1.30	24.6	0.00	fines
N-33	2.14	22.78	0.15	1.99	9.18	0.04	2.62	2.83	0.04	0.50	24.8	0.00	fines
N-34	2.00	22.30	0.17	2.08	10.14	0.04	2.71	2.87	0.05	0.88	24.2	0.00	fines
N-35	2.12	22.01	0.10	2.14	8.08	0.03	2.91	3.63	0.06	1.10	24.2	0.00	cobble
N-36	1.58	12.12	0.12	1.90	9.26	0.04	2.38	2.45	0.04	1.15	23.9	0.00	pebble
N-37	1.67	16.89	0.12	1.77	6.98	0.03	2.23	2.47	0.03	0.30	24.5	0.00	fines
N-38	1.66	17.35	0.12	1.85	6.31	0.03	2.31	2.32	0.03	1.02	24.4	0.00	cobble
N-39	1.75	14.34	0.05	1.88	6.46	0.02	2.37	2.83	0.04	1.03	23.9	0.00	fines
N-40	1.75	14.34	0.05	1.88	6.46	0.02	2.37	2.83	0.04	1.53	23.9	0.00	boulder
N-41	0.91	3.23	0.11	1.80	7.25	0.01	2.22	2.33	0.03	0.30	23.3	0.08	pebble
N-42	0.95	3.42	0.13	1.76	6.02	0.01	2.18	2.53	0.02	0.25	21.5	0.00	boulder
N-43	1.45	5.65	0.54	3.17	6.24	0.04	4.44	3.34	0.06	0.42	22.1	0.15	fines
N-44	1.75	14.34	0.05	1.88	6.46	0.02	2.37	2.83	0.04	0.69	23.9	0.00	fines
N-45	1.75	14.34	0.05	1.88	6.46	0.02	2.37	2.83	0.04	0.82	23.9	0.00	cobble
N-46	1.75	14.34	0.05	1.88	6.46	0.02	2.37	2.83	0.04	0.71	23.9	0.00	cobble
S-1	0.82	6.78	0.09	0.74	23.22	0.02	1.03	1.55	0.03	0.22	23.9	0.00	fines
S-2	1.15	10.93	0.05	1.26	11.72	0.02	1.65	2.21	0.04	0.25	23.6	0.35	fines
S-3	0.98	7.18	0.05	1.26	5.49	0.02	1.69	2.10	0.03	0.50	23.9	0.15	boulder
S-4	1.03	6.87	0.08	1.28	5.77	0.03	1.76	2.39	0.04	0.32	24.3	0.00	cobble
S-5	1.35	7.55	0.06	1.36	7.70	0.03	1.79	2.70	0.05	0.34	23.5	0.15	cobble
S-6	1.35	7.55	0.06	1.36	7.70	0.03	1.79	2.70	0.05	0.37	23.5	0.08	fines

Sites	BOD	Chla	NH ₄ N	NO ₃ N	SS	TDP	TN	TOC	TP	WD	WT	WV	Substratum
S-7	1.15	7.72	0.14	1.61	6.85	0.04	2.17	2.62	0.05	0.25	24.0	0.17	cobble
S-8	1.54	5.55	0.06	1.13	6.65	0.03	1.83	3.19	0.05	0.20	24.6	0.05	cobble
S-9	1.68	10.13	0.06	1.26	9.28	0.03	1.90	3.25	0.05	0.18	23.1	0.20	cobble
S-10	1.32	2.85	0.04	1.13	3.07	0.02	1.74	2.31	0.03	0.84	24.2	0.17	cobble
Y-1	0.68	2.25	0.06	0.80	3.23	0.02	1.15	1.89	0.02	0.60	23.3	0.24	boulder
Y-2	0.90	4.20	0.06	0.80	5.05	0.02	0.98	1.91	0.02	0.60	19.2	0.08	finer
Y-3	0.91	2.18	0.04	0.74	3.71	0.02	1.34	1.69	0.03	0.45	21.3	0.63	pebble
Y-4	1.05	2.18	0.04	0.74	5.07	0.02	1.28	2.03	0.03	0.50	22.6	0.02	pebble
Y-5	1.16	2.18	0.04	0.74	2.35	0.02	1.08	1.96	0.02	0.65	22.6	0.02	cobble
Y-6	1.43	5.64	0.02	0.65	2.63	0.02	1.01	1.41	0.02	0.70	24.1	0.02	cobble
Y-7	1.17	5.17	0.05	0.55	8.58	0.01	1.50	1.84	0.04	1.10	21.8	0.00	boulder
Y-8	0.95	2.70	0.06	0.51	2.98	0.02	0.91	1.87	0.02	0.50	22.4	0.30	boulder
Y-9	1.41	4.04	0.16	0.76	9.81	0.04	1.25	2.68	0.06	0.80	23.4	0.44	boulder
Y-10	1.44	6.62	0.07	0.80	8.56	0.03	1.22	2.92	0.05	0.70	23.7	0.05	pebble
Y-11	1.61	4.04	0.08	1.25	7.46	0.07	1.46	3.22	0.05	0.70	23.3	0.16	boulder
Y-12	1.37	0.85	0.04	0.65	1.18	0.01	0.97	1.16	0.02	0.50	22.4	0.02	boulder
Y-13	1.37	1.01	0.03	0.54	1.20	0.01	0.86	1.20	0.02	0.35	23.4	0.11	pebble
Y-14	1.54	9.48	0.21	2.02	12.16	0.07	2.72	2.17	0.09	0.55	21.5	0.00	pebble
Y-15	1.54	9.48	0.21	2.02	12.16	0.07	2.72	2.17	0.09	0.25	21.5	0.21	pebble
Y-16	1.54	9.48	0.21	2.02	12.16	0.07	2.72	2.17	0.09	1.05	21.5	0.00	finer
Y-17	2.80	20.03	0.17	1.44	10.99	0.05	2.18	4.67	0.09	0.72	23.4	0.08	finer

Sites	BOD	Chla	NH ₄ N	NO ₃ N	SS	TDP	TN	TOC	TP	WD	WT	WV	Substratum
Y-18	2.80	20.03	0.17	1.44	10.99	0.05	2.18	4.67	0.09	0.32	23.4	0.17	cobble
Y-19	3.67	46.94	0.32	1.12	15.96	0.05	2.17	3.76	0.08	1.10	24.3	0.00	finer
Y-20	4.64	33.85	3.20	2.40	10.39	0.13	6.84	4.23	0.16	0.75	24.5	0.00	finer
Y-21	5.05	53.48	3.52	2.33	10.74	0.16	7.26	4.54	0.21	0.57	25.2	0.00	boulder
Y-22	4.91	45.88	2.48	2.07	11.81	0.12	5.63	5.88	0.18	0.40	24.3	0.00	cobble
Y-23	4.28	64.97	1.73	2.13	12.22	0.09	4.90	4.19	0.13	1.05	24.7	0.00	finer
Y-24	4.28	64.97	1.73	2.13	12.22	0.09	4.90	4.19	0.13	0.25	24.7	0.00	finer
Y-25	4.03	41.39	1.30	2.13	14.20	0.08	4.39	5.42	0.13	1.00	24.0	0.00	boulder
Y-26	4.48	43.57	1.20	2.18	24.58	0.08	4.27	5.47	0.13	0.85	24.1	0.00	finer
Y-27	4.30	39.27	0.98	2.26	23.51	0.07	4.17	5.47	0.13	0.93	24.2	0.22	finer

Note: Water chemical variables were averaged from January 2012 to October 2015 from the Ministry of Environment's national water quality measurement network. Water temperature was calculated during the growing season (May–October). Water depth and water velocity were measured on the sampling date. H, Han River; G, Geum River; N, Nakdong River; S, Seomjin River; Y, Yeongsan River, BOD, Biochemical oxygen demand [mg L⁻¹]; Chla, chlorophyll *a* [mg m⁻³]; NH₄N, ammonium nitrogen [Ymg L⁻¹]; NO₃N, nitrate nitrogen [mg L⁻¹]; SS, suspended solids [mg L⁻¹]; TDP, total dissolved phosphorus [mg L⁻¹]; TN, total nitrogen [mg L⁻¹]; TOC, total organic carbon [mg L⁻¹]; TP, total phosphorus [mg L⁻¹]; WD, water depth [m]; WT, water temperature [°C]; WV, water velocity [m s⁻¹]; Substratum, representative substratum.

국문 초록

최근 한국의 하천 생태계는 유수 환경에서 정수 환경으로 크게 변화하였고 침수식물이 하천 본류에 넓게 정착하였다. 침수식물의 중요성에도 불구하고, 빠른 속도로 확산하고 밀도 높게 서식하는 침수식물은 하천 생태계에 해로운 영향을 끼친다. 침수식물의 종 구성과 침수식물과 관련된 환경인자를 함께 이해하는 것은 하천 생태계 관리를 위해서 중요하다. 본 연구는 침수식물과 환경인자와의 관계를 밝히는데 초점을 두었다. 2014년과 2015년 5월부터 9월 사이에 한강 71곳, 금강 43곳, 낙동강 46곳, 영산강 27곳, 섬진강 10곳 (총 197곳)의 본류와 지류에서 침수식물 식생과 수환경을 조사하였다. 전체 조사지에서 총 12종의 침수식물인 붕어마름, 검정말, 이삭물수세미, 나자스말, 민나자스말, 말즘, 새우가래, 대가래, 애기가래, 말, 실말, 나사말이 분포하였다. 이 중에서 검정말, 이삭물수세미, 말즘이 전체 조사지에서 가장 우점하였다. 유사도 분석 결과, 한강, 금강, 낙동강, 영산강 간의 수환경과 출현 식물종은 유사하였으나 침수식물의 발생 빈도는 강 별로 다르게 나타났다. 하지만 암모니아성 질소, 질산성 질소, 총 질소 농도는 강 별로 통계적으로 유의미한 차이를 보였다. 특히, 한강은 다른 강들에 비해서 암모니아성 질소의 농도가 높았으며 영산강은 다른 강들에 비해서 질산성 질소와 총 질소의 농도가 낮았다. 침수식물의 서식 유무와 관련 있는 환경인자는 생화학적 산소요구량, 클로로필 a , 부유물질, 생육기간의 수온과 같은 빛 이용과 관련된 인자로

밝혀졌으며, 영양염류 농도는 서식 유무와 관련하여 주요 인자가 아닌 것으로 사료된다.

한강 (양평 조사지)과 낙동강 (상주 조사지)의 각 대표 지점에서 3년간의 모니터링 결과, 두 장소 모두에서 민나자스말이 빠르게 정착하였고 주요종이 되었다. 검정말, 이삭물수세미, 붕어마름, 말즘 군집의 다양도지수 비교 결과, 나사말 군집의 식물 종들이 비교적 균등한 피도를 보였으며 가장 높은 다양도지수를 나타냈다. 일반화 선형 모델로부터 암모니아성 질소, 질산성 질소 농도, 유속이 Shannon 다양도 지수와 종 풍부도에 영향을 끼치는 인자라는 것을 알 수 있었다. Shannon 다양도지수와 종 풍부도는 영양염류 농도가 높고 유속이 빨라질수록 감소하였다. 이 결과는 생산성과 교란이 적은 환경에서 침수식물 군집의 다양도지수가 높다는 것을 의미한다.

일반화 가법 모형을 이용하여 조사지에서 가장 우점하고 있는 검정말과 이삭물수세미의 잠재 서식처의 환경인자를 규명하였다. 이삭물수세미의 잠재 서식처는 클로로필 a 농도, 질산성 질소 농도, 부유물질 농도, 수온, 수심, 유속과 관련이 있었다. 검정말의 잠재 서식처는 전기전도도 농도, 부유물질 농도와 관련이 있었다. 침수식물의 산포와 종 구성은 수질뿐만 아니라 유속에 의해 영향을 받기 때문에 하천 생태계에서 침수식물과 수환경을 모니터링 하는 것은 중요하다. 침수식물 다양도 유지와 적절한 수준의 침수식물 우점도를 조절하기 위해서는 다양한 수문학적 특징을 지닌 유동 하천으로서의 관리가 필요하다. 본 연구의 결과들은 대형 보 건설 이후의 하천 생태계 관리를 위해 필요한 4대강의 초기 침

수식물 분포 현황과 잠재 서식처 예측에 대한 정보를 제공한다.

주요어: 하천생태계, 침수식물, 수환경, 검정말, 이삭물수세미

학번: 2012-30085